

The Subfamily Littorininae (Gastropoda: Littorinidae) in the Temperate Southern Hemisphere: The Genera *Nodilittorina*, *Austrolittorina* and *Afrolittorina*

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ABSTRACT. The littorinine gastropods of the temperate southern continents were formerly classified together with tropical species in the large genus *Nodilittorina*. Recently, molecular data have shown that they belong in three distinct genera, *Austrolittorina*, *Afrolittorina* and *Nodilittorina*, whereas the tropical species are members of a fourth genus, *Echinolittorina*. *Austrolittorina* contains 5 species: *A. unifasciata* in Australia, *A. antipodum* and *A. cincta* in New Zealand, and *A. fernandezensis* and *A. araucana* in western South America. *Afrolittorina* contains 4 species: *A. africana* and *A. knysnaensis* in southern Africa, and *A. praetermissa* and *A. acutispira* in Australia. *Nodilittorina* is monotypic, containing only the Australian *N. pyramidalis*. This paper presents the first detailed morphological descriptions of the African and Australasian species of these three southern genera (the eastern Pacific species have been described elsewhere). The species-level taxonomy of several of these has been confused in the past; *Afrolittorina africana* and *A. knysnaensis* are here distinguished as separate taxa; *Austrolittorina antipodum* is a distinct species and not a subspecies of *A. unifasciata*; *Nodilittorina pyramidalis* is separated from the tropical *Echinolittorina trochoides* with similar shell characters. In addition to descriptions of shells, radulae and reproductive anatomy, distribution maps are given, and the ecological literature reviewed.

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The Littorinidae are among the most intensively studied families of marine gastropods and their systematics has been the subject of much research. As new techniques and tools have become available over the past 30 years, systematists have applied them to littorinids, with the result that the classification of the group has been repeatedly updated and refined. As late as 1970, the classification used by Rosewater (1970) was one in which both species and genera were defined principally by features of their shells. In the following decade the use of reproductive anatomy, morphometrics and electrophoresis began to result in recognition of new species (Heller, 1975; Hannaford Ellis,

1979). Information from scanning electron microscopy of radulae, light microscopy of sperm and from fine dissection was soon employed to redefine the traditional genera (Bandel & Kadolsky, 1982; Reid, 1986), and a cladistic analysis of the family was attempted (Reid, 1989). This served as the basis of a phylogenetic classification that has since become current in the systematic literature. Direct sequencing of DNA is now routine, and molecular phylogenetic trees have been produced for a few littorinid clades, notably the genera *Littorina* (Reid *et al.*, 1996) and *Tectarius* (Reid & Geller, 1997). Recently, the phylogeny and classification of the subfamily Littorininae was tested

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with DNA-sequence data, resulting in significant changes to the scheme (Williams *et al.*, 2003). Although changing concepts of littorinid species and genera may be confusing to non-systematists, these refinements represent progress towards a phylogenetic system in which definitions of species will be informed by genetics as well as morphology, and generic groupings will accurately reflect evolutionary relationships.

Among the littorinids most affected by changing classifications are those that have become familiar under the generic name *Nodilittorina* (Bandel & Kadolsky, 1982; Reid, 1989). The taxonomic history of this group is complex (Reid & Geller, 1997; Reid, 2002a,b; see Taxonomic History below). The name was introduced as a subgenus, for those *Littorina* species with nodulose shell sculpture, paucispiral operculum and unmodified aperture (von Martens, 1897). It was first treated as a genus by Abbott (1954) who, in the first anatomical account, noted close similarity with some *Littorina* (*Melarhaphé*) species with smooth, striate shells. Nevertheless, Rosewater (1970) retained an essentially shell-based generic classification, placing only nodulose species in *Nodilittorina*. Species with smooth shells were retained in the large genus *Littorina*, although he created the new subgenus *Austrolittorina* for those with penial anatomy resembling *Nodilittorina*. With increasing emphasis on the significance of radulae and anatomy, shell sculpture was recognized as a poor guide to relationships, and *Austrolittorina* was synonymized with *Nodilittorina* (Bandel & Kadolsky, 1982). It was not clear that this was a natural group, for in a cladistic analysis of available morphological characters only one non-unique synapomorphy was discovered, the colour pattern of the cephalic tentacles (Reid, 1989). However, this classification was widely adopted. The most recent review listed 60 members of *Nodilittorina*, the great majority of them distributed in the tropics (Reid, 2002b). A parsimony analysis of morphological characters of all known *Nodilittorina* species produced a poorly resolved tree, but suggested that a group of nine or ten species, all occurring in the temperate regions of the southern hemisphere, shared the apparent synapomorphy of an additional loop of the egg groove through the capsule gland in the pallial oviduct (Reid, 2002b). Furthermore, this “southern-temperate group” was reconstructed as sister to the northern-temperate genus *Littorina*, and nested within

Nodilittorina. This implied that *Nodilittorina* was not a monophyletic clade, but because the phylogenetic reconstruction was based on relatively few available characters, the conclusion was tentative.

The suggestion of a group of southern-temperate *Nodilittorina* species was of more than purely phylogenetic and taxonomic importance. The species involved (two from southern Africa, four from Australia, two from New Zealand, two from the Pacific coast of South America) are abundant members of the littoral fauna, well studied by marine biologists (review by McQuaid, 1996a,b). Their possible relationship raised interesting biogeographic questions of the origin of similarities among the marine organisms of the southern continents. Furthermore, a possible sister-relationship with *Littorina* implied an antitropical distribution pattern. The phylogeny of the entire subfamily Littorininae was therefore reexamined with DNA-sequence data, with surprising results (Williams *et al.*, 2003). The genus *Nodilittorina* was shown to be polyphyletic, consisting of four distinct clades (Fig. 1) that must be recognized as genera (because they are of equivalent rank to other well established littorinid genera). The largest of these (*Echinolittorina*) is composed of more than 50 species of almost entirely tropical distribution. The southern-temperate species fall into three groups: one distributed in Australia, New Zealand and South America (five species of *Austrolittorina*), a second in southern African and Australia (four species of *Afrolittorina*) and a third in Australia alone (the monotypic *Nodilittorina sensu stricto*). As a consequence of these changing ideas of classification and phylogenetic relationship, the common Australian species “*Littorina*” *unifasciata* has, in just over 30 years, been variously classified as *Littorina* (*Melarhaphé*), *Littorina* (*Austrolittorina*), *Nodilittorina* and *Austrolittorina*. Recent generic assignments are summarized in Table 1.

Significant changes have also taken place in the species-level classification of the southern-temperate littorinines (Table 1). The most recent monographic treatment of the Indo-West Pacific Littorininae was that of Rosewater (1970). His species concepts were broad and based to a large degree on resemblances among shells. At least two nodulose species of *Echinolittorina* were included in his description of *Nodilittorina pyramidalis*, as pointed out by Reid (1989, 1992). Rosewater considered *Littorina unifasciata* to be a

Table 1. Summary of generic classification of southern-temperate Littorininae and species that have been confused with them. Generic and subgeneric abbreviations used in this table: Af., *Afrolittorina*; Au., *Austrolittorina*; E., *Echinolittorina*; L., *Littorina* (but subgenus *Littoraria* not abbreviated); N., *Nodilittorina*.

species	Rosewater (1970)	Reid (1989)	Reid (2002a)	Williams <i>et al.</i> (in press)
<i>pyramidalis</i>	<i>N. pyramidalis pyramidalis</i>	<i>N. (N.) pyramidalis</i>	<i>N. pyramidalis</i>	<i>N. pyramidalis</i>
<i>trochoides</i>	<i>N. pyramidalis pyramidalis</i>	<i>N. (N.) trochoides</i>	<i>N. trochoides</i>	<i>E. trochoides</i>
<i>pascua</i>	<i>N. pyramidalis pascua</i>	<i>N. (N.) pascua</i>	—	<i>E. pascua</i>
<i>unifasciata</i>	<i>L. (Au.) unifasciata unifasciata</i>	<i>N. (N.) unifasciata</i>	<i>N. (Au.) unifasciata</i>	<i>Au. unifasciata</i>
<i>fernandezensis</i>	<i>L. (Au.) unifasciata fernandezensis</i>	<i>N. (N.) fernandezensis</i>	<i>N. (Au.) fernandezensis</i>	<i>Au. fernandezensis</i>
<i>antipodum</i>	<i>L. (Au.) unifasciata antipodum</i>	<i>N. (N.) antipodum</i>	<i>N. (Au.) antipodum</i>	<i>Au. antipodum</i>
<i>cincta</i>	<i>L. (Au.) cincta</i>	<i>N. (N.) cincta</i>	<i>N. (Au.) cincta</i>	<i>Au. cincta</i>
<i>araucana</i>	<i>L. (Au.) araucana</i>	<i>N. (N.) araucana</i>	<i>N. araucana</i>	<i>Au. araucana</i>
<i>africana</i>	<i>L. (Au.) africana</i>	<i>N. (?E.) africana</i>	<i>N. (Au.) africana</i>	<i>Af. africana</i>
<i>knysnaensis</i>	<i>L. (Au.) knysnaensis</i>	<i>N. (?E.) ?africana</i>	<i>N. (Au.) knysnaensis</i>	<i>Af. knysnaensis</i>
<i>praetermissa</i>	<i>L. (Littoraria) praetermissa</i>	<i>N. (?N.) praetermissa</i>	<i>N. (Au.) praetermissa</i>	<i>Af. praetermissa</i>
<i>acutispira</i>	<i>L. (?Littoraria) acutispira</i>	<i>N. (?N.) acutispira</i>	<i>N. (Au.) acutispira</i>	<i>Af. acutispira</i>

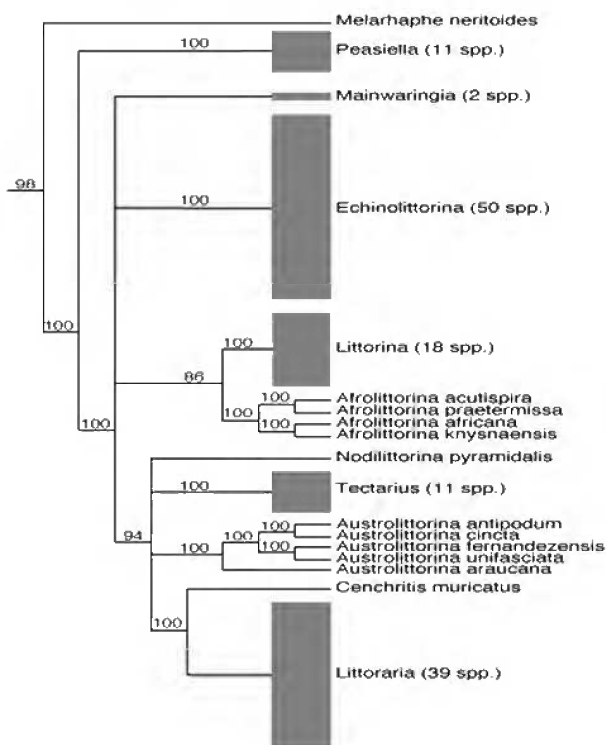


Fig. 1. Summary of molecular phylogeny of Littorininae, with species-level relationships shown for *Austrolittorina* and *Afrolittorina*, produced by Bayesian analysis of combined sequence data from 28S, 18S, 12S and COI genes; nodes supported by posterior probabilities less than 85% have been collapsed. Redrawn from Williams *et al.* (2003). Numbers of species are totals of known species for each genus (Williams *et al.*, 2003, used fewer taxa as exemplars of these genera, but they are believed to be monophyletic); other genera are monotypic as shown.

temperate Pacific species with subspecies *unifasciata*, *antipodum* and *fernandezensis* in Australia, New Zealand and the Juan Fernández Islands respectively; these were later listed as distinct species of *Nodilittorina*, but without discussion (Reid, 1989). New data on egg-capsule morphology (Rudman, 1996) and a full description of *N. fernandezensis* (Reid, 2002a) supported this decision. The status of the two southern African species has also been disputed. Rosewater (1970) recognized both *Littorina africana* and *L. knysnaensis*, but these were later synonymized (Hughes, 1979; doubtfully by Reid, 1989), before once more being listed as distinct (Reid, 2002b). Of the ten southern-temperate littorinine species considered here, the definitions of only three have remained unchanged since the monograph of Rosewater (1970; see also Ponder & Rosewater, 1979) (*Austrolittorina cincta*, *Afrolittorina praeterrimissa*, *Afrolittorina acutispira*). Furthermore, anatomical characters of eight of the species have not been adequately described and illustrated; only *Austrolittorina fernandezensis* and *A. araucana* have received a full anatomical description (Reid, 2002a).

The aim of the present study is to present the first full descriptions of the eight southern-temperate littorinines that are poorly known anatomically, and to clarify their status as distinct species. These are *Nodilittorina pyramidalis*, *Austrolittorina unifasciata*, *Austrolittorina antipodum*,

Austrolittorina cincta, *Afrolittorina africana*, *Afrolittorina knysnaensis*, *Afrolittorina praeterrimissa* and *Afrolittorina acutispira*. This will confirm the morphological characters of the genera *Nodilittorina*, *Austrolittorina* and *Afrolittorina* that were recently defined as a result of a molecular phylogenetic analysis (Williams *et al.*, 2003). In addition, the large taxonomic and ecological literature on these species will be reviewed and detailed distribution maps given. For completeness, diagnoses of the two remaining species of *Austrolittorina* are included (*A. fernandezensis* and *A. araucana*), although these have been fully described elsewhere (Reid, 2002a).

General discussion of the comparative morphology, biogeography and evolutionary radiation of these groups can be found in Reid (2002b) and Williams *et al.* (2003). Although the genera *Austrolittorina* and *Afrolittorina* have been clearly shown to be monophyletic clades by the analysis of DNA-sequence data, their relationships (and those of the monotypic *Nodilittorina pyramidalis*) with other littorinine genera remain poorly resolved (Williams *et al.*, 2003). It is, however, possible that the southern oceans have been a focus for the evolution of littorinines, and that these genera are not merely offshoots of a predominantly tropical radiation, contradicting earlier ideas (Reid, 1989). It is unfortunate that none of the three genera considered here has a pre-Pleistocene fossil record, so that hypotheses of their biogeographic history remain speculative. Based on imprecise molecular estimates of age, Williams *et al.* (2003) suggested that the family Littorinidae was older than had been supposed, and that *Austrolittorina* and *Afrolittorina* were ancient genera that were present on the shores of Gondwana as early as the Upper Cretaceous. This remains to be tested by the discovery of new fossil material.

Material and methods

This study is based on examination of all material in the collections of the following institutions: Australian Museum, Sydney (AMS), Natural History Museum, London (BMNH), National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), Muséum National d'Histoire Naturelle, Paris (MNHN), Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSNB), Zoölogisch Museum, Amsterdam (ZMA) and National Museum of Wales, Cardiff (NMW). Additional material has been examined on loan from the following: Natal Museum, Pietermaritzburg (NM), South African Museum, Cape Town (SAM) and Museum of New Zealand Te Papa Tongarewa, Wellington (MNZ). All available primary type material from these institutions was examined, and also from Tasmanian Museum and Art Gallery, Hobart (TMAG), Staatliches Museum für Naturkunde Stuttgart (SMNS) and Oxford University Museum (OM). Other (almost entirely secondary) type material is housed in additional museums: Natur-Museum Senckenberg (SMF), Swedish Museum of Natural History, Stockholm (SMNH), Museum of Comparative Zoology, Harvard University (MCZ) and Auckland Museum (AM), but was not examined. Personal collections were made in South Africa (1970–1972), Australia (1980–1984), New Zealand (1981) and Chile (1998), and are deposited in BMNH. In total, 650 samples were examined of the eight species described here in detail (for the two additional members of *Austrolittorina*, *A. araucana* and *A. fernandezensis*, see Reid, 2002a).

Shell dimensions were measured with vernier callipers to 0.1 mm. Shell height (H) is the maximum dimension parallel to the axis of coiling, shell breadth (B) the maximum dimension perpendicular to H, and the length of the aperture (LA) the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip. Shell shape was quantified as the ratios H/B and H/LA (relative spire height, SH), and the range of these ratios is given. The parietal area adjacent to the aperture may show evidence of dissolution by the mantle edge, producing a crescentic eroded area. In descriptions of shell sculpture, primary grooves are incised spiral lines or grooves that are visible on the early teleoconch whorls. On the spire the primary grooves are counted between successive sutures, but on the last whorl they are counted from the suture to the periphery of the whorl (so that one or more extra grooves are visible). If the periphery is not well marked, grooves are counted over the entire last whorl, from suture to base. If present, secondary grooves appear by interpolation, usually on the penultimate or final whorl. The spaces between the grooves are referred to as ribs, whether or not they are strongly raised. Microstriae are fine incised spiral lines that cover the entire surface and are visible only under low magnification. The periphery is the junction between the upper part of the final whorl and the base of the shell; is usually marked by a slight angulation, or by an enlarged rib. The suture generally runs one or two ribs above the periphery, or is situated at the peripheral rib. Protoconchs are rarely preserved; where possible the whorls were counted as described by Reid (1996). The opercular ratio describes the coiling of the operculum, and is the ratio of two parallel measurements, the diameter of the spiral part divided by the maximum length (Reid, 1996).

Living animals were relaxed in 7.5% (volume of hydrated crystals to volume of fresh water) magnesium chloride solution. Animals were fixed in 10% seawater formalin buffered with borax, and stored in 80% ethanol. The most important anatomical characters for taxonomic purposes are the penis and oviduct; drawings of these were made by camera lucida and drawing conventions are indicated in Fig. 3. For general accounts of the anatomy of littorinids see Reid (1986, 1989, 1996). Sperm samples were removed from the seminal vesicles of relaxed, living animals, fixed in 0.5% seawater formalin, examined immediately by light microscopy, and drawn by camera lucida. Alternatively, sperm were removed from specimens fixed and stored in formalin, but not from material stored in ethanol (in which shrinkage of paraspermatozoa by about 20% occurs, Reid, 1996).

Radulae are relatively uniform in these littorinine species (with the exception of *Afrolittorina acutispira*) and therefore not useful for identification. At least three radulae were examined from each species. The relative radular length is the total radular length divided by shell height. Radulae were cleaned by soaking in a hypochlorite bleaching solution at room temperature for about 5 min, rinsed in distilled water, mounted on a film of polyvinyl acetate glue on glass, allowed to dry in air, and coated with gold and palladium before examination with a scanning electron microscope. Unworn portions of the radula were viewed in three orientations: in standard flat view from vertically above the radula (to show shapes of tooth bases), at an angle of 45° from the front end (to show shape of tooth cusps), and at an angle of 45° from the side (to show relief). The shape

of the rachidian (central) tooth was quantified as the ratio of the total length (in flat view) to maximum basal width. Numbers and relative sizes of cusps are not given for the five central teeth in each row, because these do not vary: three cusps on rachidian (largest central); four cusps on each of lateral and inner marginal (largest is third from inside in each case). All species show flanges on inside and outside of base of outer marginal tooth.

Synonymies are not exhaustive, but attempt to list all new names (including nomina nuda) and new combinations, major taxonomic works and faunistic lists, standard identification guides, and significant morphological descriptions. One lectotype has been designated in a case where syntypes were not conspecific, and one figure has been designated as lectotype for a valid name.

Distribution maps were plotted from the material examined, with the addition of literature records as indicated, where these extend the known range and were considered reliable. Localities are listed only when they are range limits or are of other biogeographic significance. Complete locality lists are available from the authors on request.

Systematics

Littorinidae Anon., 1834

Nodilittorina von Martens, 1897

Littorina (*Nodilittorina*) von Martens, 1897: 204 (type *Littorina pyramidalis* Quoy & Gaimard, 1833, by subsequent designation, Abbott, 1954: 451).

Taxonomic history. The name *Nodilittorina* was introduced by von Martens (1897) as a subgenus for those *Littorina* species with nodulose shell sculpture, but lacking the many-whorled circular operculum and apertural tooth characteristic of *Tectus* (now *Tectarius*, see Reid & Geller, 1997). In the influential classification of Thiele (1929; followed by Wenz, 1938; Clench & Abbott, 1942), *Nodilittorina* appeared as a subgenus of *Tectarius*, because of the narrow rachidian tooth. It was first used as a full genus by Abbott (1954), on the basis of comparisons of penes, radulae and egg capsules of *Nodilittorina tuberculata* (Menke, 1828) (now *Echinolittorina tuberculata*) with those of other littorinids. He did also note the “*Nodilittorina*-like” penes of *Littorina* (*Melarthaphe*) *mauritiana* (Lamarck, 1822) (a misidentification of *Austrolittorina unifasciata*, see synonymy of that species below) and *L. (M.) ziczac* (Gmelin, 1791) (now *Echinolittorina ziczac*), in the first indication that *Nodilittorina* might include species without nodulose shells. Nevertheless, in his monograph of Indo-Pacific species, Rosewater (1970) still emphasized shell sculpture above anatomical characters, and included only species with nodulose or granulose sculpture in *Nodilittorina*. Smooth-shelled species with penes resembling those of *Nodilittorina* (i.e. with single mamilliform gland and adjacent glandular disc, in terminology of Reid, 1989) were placed in a new subgenus, *Littorina* (*Austrolittorina*). The first attempt to revise the classification of littorinids taking into account all available anatomical evidence was by Bandel & Kadolsky (1982). The main features of their diagnosis of *Nodilittorina* were: spirally striate, nodulose or granulose shell; pale basal band in aperture; narrow rachidian tooth; pelagic egg

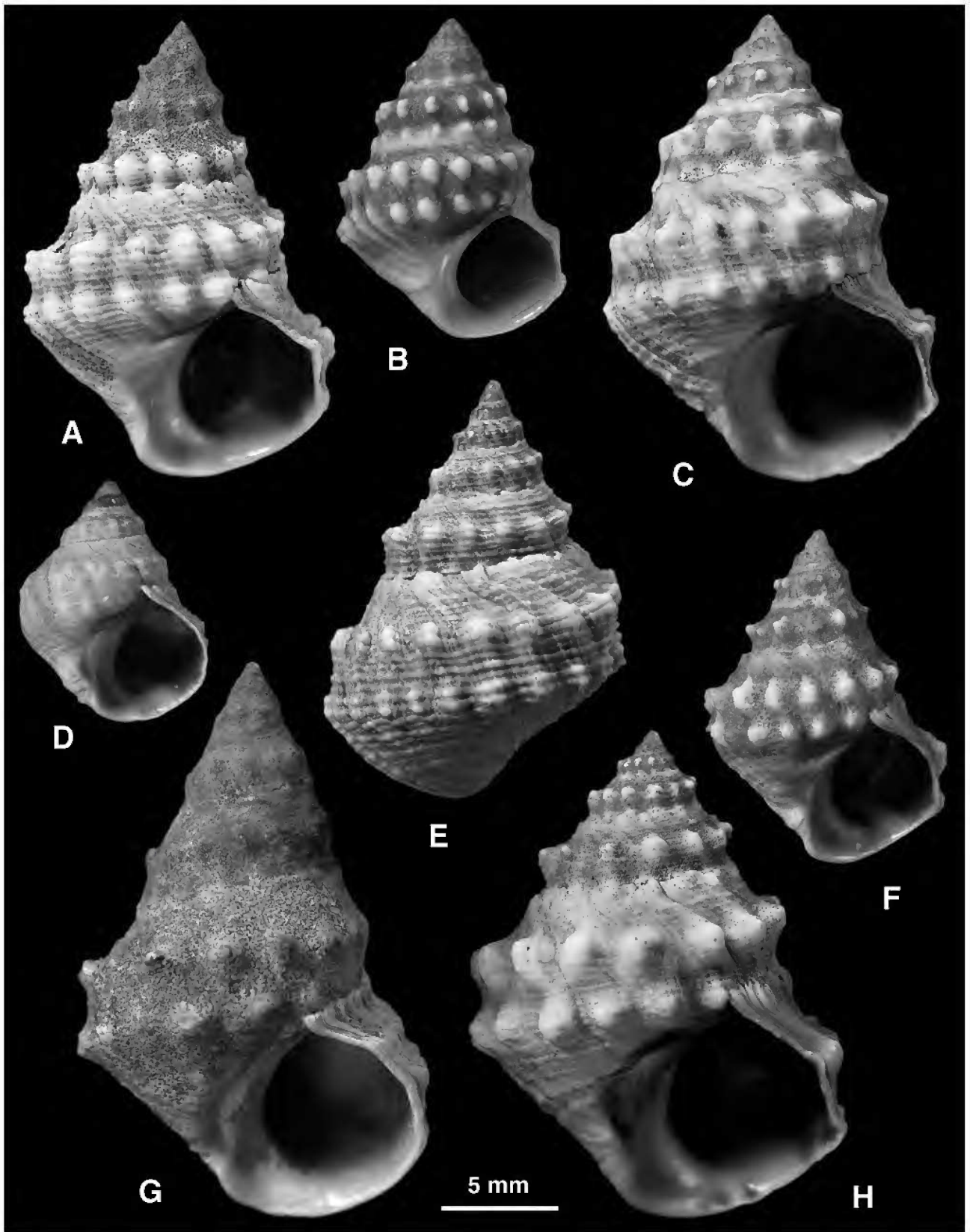


Fig. 2. *Nodilittorina pyramidalis*: (A) Jervis Bay, NSW, Australia (BMNH 1928.4.30.55). (B, F) Great Keppel Island, Queensland, Australia (AMS C089660). (C) Karuah, NSW, Australia (BMNH 20030388). (D) Alexandra Headland, Queensland, Australia (BMNH 20030389). (E) Long Reef, Collaroy, NSW, Australia (AMS C177413). (G) Lectotype of *Littorina pyramidalis* Quoy & Gaimard, 1833; Jervis Bay, NSW, Australia (MNHNP unreg.). (H) Lord Howe Island (AMS C089673).

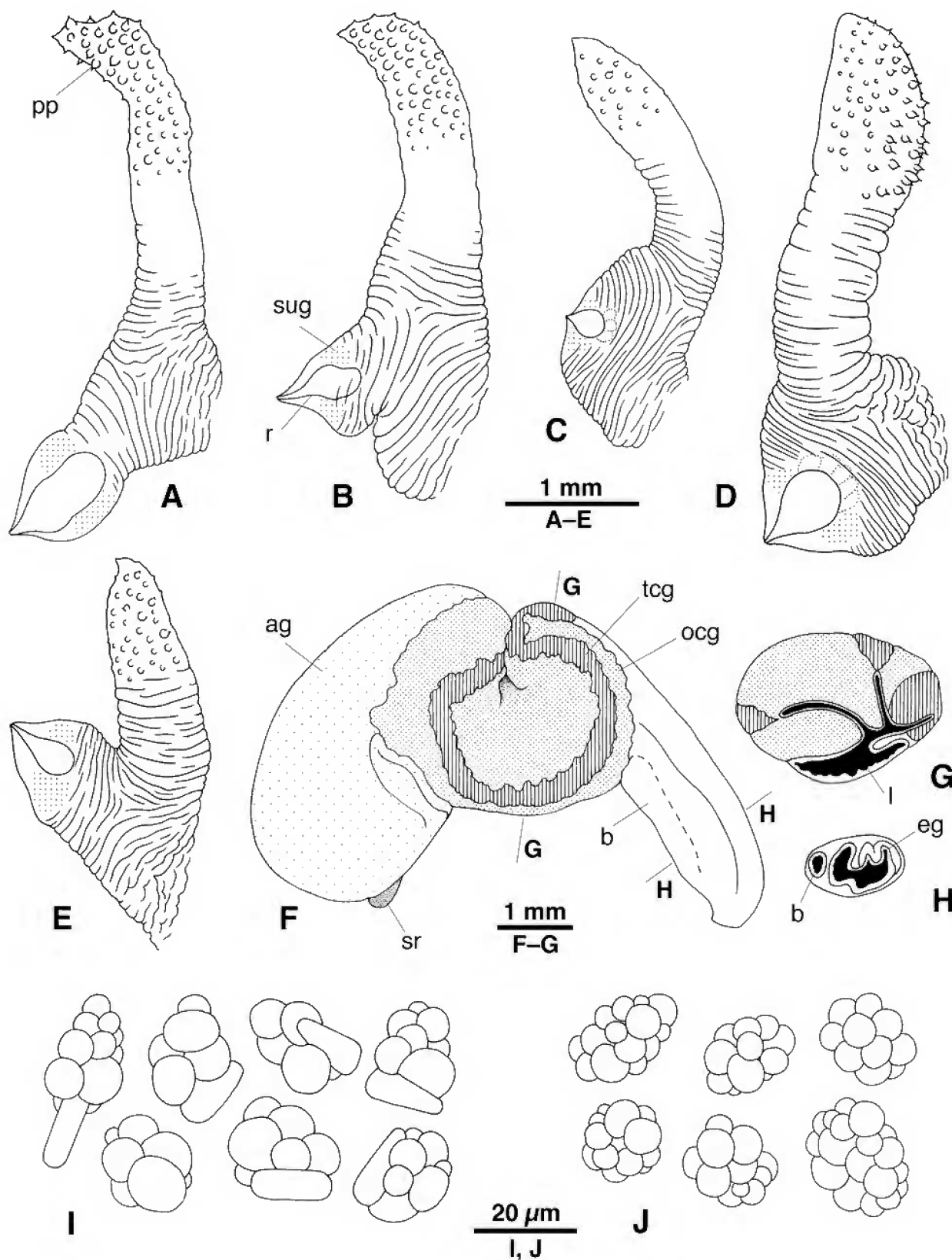


Fig. 3. *Nodilittorina pyramidalis*: (A–E) Penes. (F) Pallial oviduct with transverse sections (G,H). (I,J) Paraspermatozoa from two specimens. (A,B) Mollymook, NSW, Australia (BMNH 20030390). (C) Fairlight, Sydney, NSW, Australia (BMNH 20030391). (E,I,J) North Harbour, Sydney, NSW, Australia (BMNH 20030392). (F–H) Mullimburra Point, NSW, Australia (AMS C356720). Shell heights: (A) 12.0 mm; (B) 11.1 mm; (C) 10.3 mm; (D) 15.0 mm; (E) 12.0 mm; (F) 17.0 mm. Abbreviations: (ag) albumen gland; (b) copulatory bursa (visible by transparency); (eg) egg groove; (ocg) opaque capsule gland; (pp) penial papillae; (r) receptacle of mamilliform penial gland (visible by transparency); (sr) seminal receptacle; (sug) subepithelial glandular tissue (visible by transparency, not a discrete penial glandular disc); (tcg) translucent capsule gland.

capsule sculptured with spiral ridges; penis variable, but often with single mamilliform gland and glandular disc. This definition greatly increased the number of species, because it included the smooth, striate forms formerly classified as *Littorina* (*Austrolittorina*). It was essentially supported, with some modifications, by new anatomical information on paraspermatozoa and pallial oviducts (Reid, 1986, 1989). This broad definition has persisted in the taxonomic literature (Reid, 2001, 2002a) and the most recent review listed 60 species of *Nodilittorina* (Reid, 2002b).

However, a rigorous phylogenetic definition of the genus has proved elusive, suggesting that this large group is not a monophyletic one. The first attempt at a parsimony analysis of morphological characters of the Littorinidae included four exemplars of *Nodilittorina*, and only a single, non-unique synapomorphy was discovered for the genus, the banding pattern of the cephalic tentacles (Reid, 1989). A recent analysis of the morphological characters of all 60 species then included in *Nodilittorina* produced a poorly resolved tree, in which all but two *Nodilittorina* species formed a paraphyletic group within a clade that also included the genus *Littorina sensu stricto* (Reid, 2002b). This *Nodilittorina* plus *Littorina* clade was defined by the one unique and unequivocal synapomorphy of the form of the outer marginal radular teeth (with a flange on either side of the base), although this character state was reconstructed as lost within *Littorina*. According to this interpretation, all other features previously used to characterize *Nodilittorina* were plesiomorphic similarities and without phylogenetic significance. Analysis of DNA sequence data has now shown unequivocally that *Nodilittorina* in the broad sense is not a monophyletic group, and has supported the integrity of three distinct clades: a large clade of 50 tropical species (for which the name *Echinolittorina* is available), a clade of five species from Australia, New Zealand and South America (a restricted use of Rosewater's genus *Austrolittorina*), and a clade of four species from southern Africa and Australia (for which the new name *Afrolittorina* was established) (Williams *et al.*, 2003). There was no strong support for the inclusion of the remaining species, *Nodilittorina pyramidalis*, in these or other generic-level clades. This is the type species of the genus (Abbott, 1954) and it is therefore appropriate to treat *Nodilittorina* as monotypic.

From the perspective of stability of taxonomic usage of the generic name *Nodilittorina*, the identity of its type species is unfortunate. The designation of *N. pyramidalis* as the type species has a confused history. Under his original description of *Littorina* (*Nodilittorina*) von Martens (1897) listed the names *nodulosa* Pfeiffer, *dilatata* d'Orbigny, *trochiformis* Dillwyn, *antonii* Philippi and *granosa* Philippi, he gave a detailed description of *L. vilis* Menke, and gave notes on *L. pyramidalis* Quoy & Gaimard, *L. natalensis* Krauss in Philippi and *L. subnodosa* Philippi. The first designation of a type species was by Wenz (1938) who, without discussion, gave the type as "*T. (N.) nodulosus* (Gmelin) [*Turbo*]". Abbott (1954) rejected this designation as invalid, on the grounds that *Turbo nodulosus* Gmelin, 1791 was not among the species included by von Martens (1897) and because it is a turbinid species. (In fact it is an *Angaria*; the littorinid species that Wenz presumably intended was *Trochus nodulosus* Gmelin, 1791.) Abbott (1954, following Clench & Abbott, 1942) interpreted

"*nodulosa* Pfeiffer", as listed by von Martens (1897), as the species now classified as *Tectarius* (*Tectininus*) *antonii* (Philippi, 1846), whereas he believed *Trochus nodulosus* Gmelin to be based on both *N. dilatata* and *N. pyramidalis*. However, as pointed out by Kadolsky (1971; Bandel & Kadolsky, 1982), Pfeiffer was not in fact the author of the name *nodulosa* as listed by von Martens (1897), but only of the new combination *Littorina nodulosa* (Gmelin). A case might therefore be made that Wenz's (1938) designation was valid, although this could be dismissed on the technicality of his mistaken use of the original genus *Turbo*. Gmelin's species *Trochus nodulosus* is based on figures by Chemnitz (1781) that are here interpreted to represent the species currently classified as *Echinolittorina trochoides* (Gray, 1839) (see Taxonomic History of *N. pyramidalis* below). Rejecting Wenz's designation of this species, Abbott (1954) instead proposed *Littorina pyramidalis* as the type of *Nodilittorina*. Abbott himself believed this to be the earliest valid name for a species that included the two taxa now recognized as *N. pyramidalis* and *E. trochoides* (*Trochus nodulosus* Gmelin is unavailable, as it is a junior homonym of *T. nodulosus* Solander, 1766). He therefore probably aimed to fulfil the intention of Wenz. Although to allow Wenz's (1938) designation would preserve *Nodilittorina* more nearly in its accustomed usage, it seems preferable to accept the designation by Abbott (1954). This avoids the doubt surrounding the identity of Gmelin's species. Furthermore, *N. pyramidalis* has been accepted as the type species for nearly 50 years, even if it has been frequently misidentified during that time.

Further details of the history of the usage of *Nodilittorina*, including subgeneric divisions and inclusion of species now assigned to other genera, are available elsewhere (Reid & Geller, 1997; Reid, 2002a,b).

Diagnosis. Shell nodulose; nodules not axially aligned; eroded parietal area; no pseudombilicus; unpatterned. Cephalic tentacles with 2 broad black longitudinal stripes. Penis with swollen filament bearing numerous minute papillae; base bifurcate; single mamilliform gland surrounded by subepithelial glandular tissue (not separated as distinct glandular disc or flap); penial vas deferens an open groove. Paraspermatozoa with small rod bodies. In pallial oviduct egg groove makes a simple loop through albumen gland, circular loop through capsule gland, no loop in jelly gland; copulatory bursa opens in anterior position near anterior end of pallial oviduct. (After Williams *et al.*, 2003.)

Nodilittorina pyramidalis (Quoy & Gaimard, 1833)

Figs. 2–3, 4A,B, 5

- Littorina pyramidalis* Quoy & Gaimard, 1833: 482–483, pl. 33, figs. 12–13, figs. 14–15 (tentacles and foot) (Baie Jervis, Nouvelle-Hollande [Jervis Bay, New South Wales, Australia]; lectotype (Rosewater, 1970) (fig. 2G), 1 dry paralectotype, 2 paralectotypes in alcohol, MNHNP, seen). Deshayes, 1843: 210. Reeve, 1857: *Littorina* sp. 14, pl. 2, fig. 14. Tenison Woods, 1879: 69–71.
- Littorina pyramidalis*.—Philippi, 1846: 143, *Littorina* pl. 2, figs. 10, 12.
- Tectarius pyramidalis*.—Adams & Adams, 1854: 315. Angas, 1867: 209. Hedley, 1918: M51.
- Littorina* (*Tectus*) *pyramidalis*.—Nevill, 1885: 156.
- Littorina* (*Nodilittorina*) *pyramidalis*.—von Martens, 1897: 205.

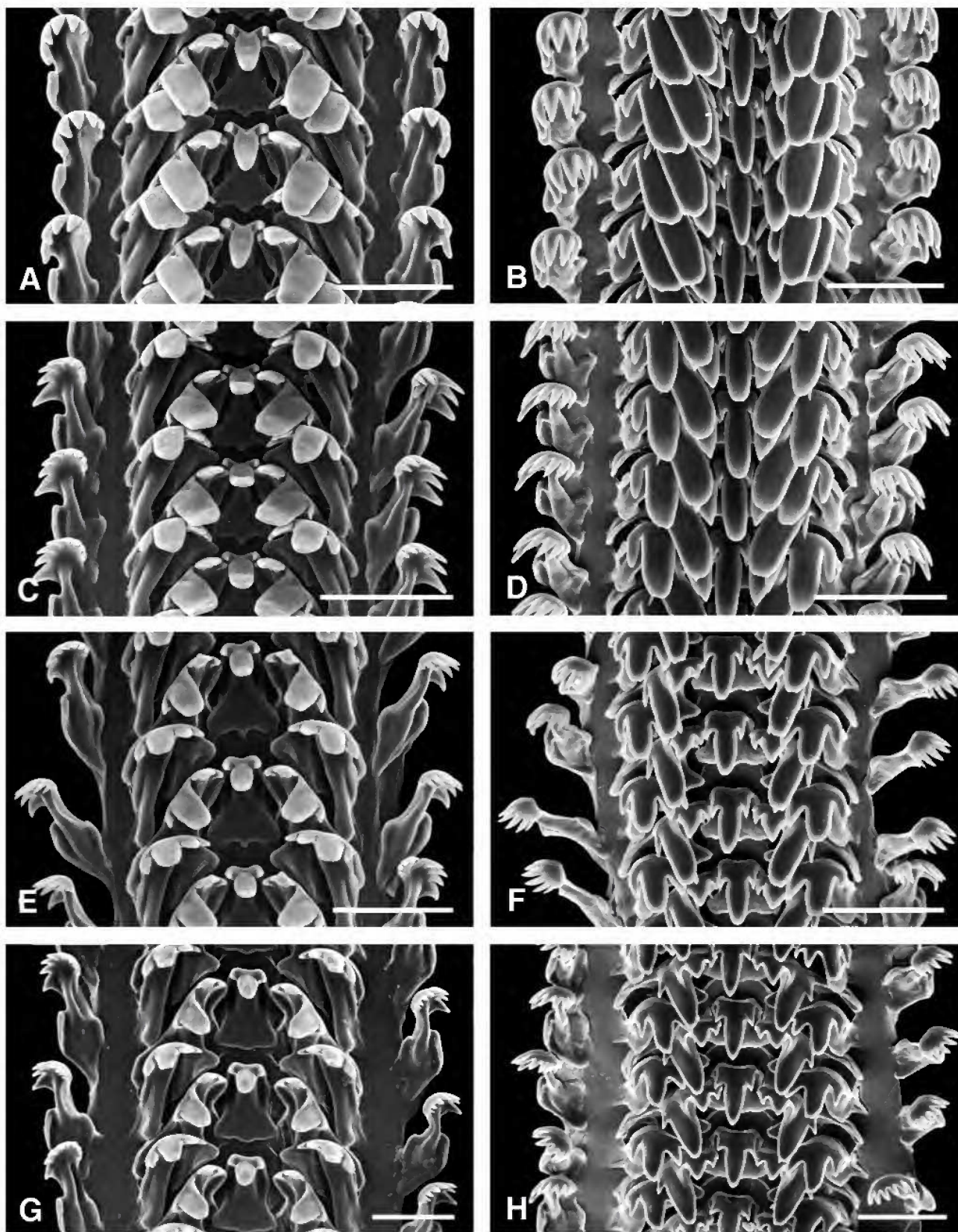


Fig. 4. Radulae; views of same specimen flat (A,C,E,G) and at 45° from anterior end (B,D,F,H). (A,B) *Nodilittorina pyramidalis*, Mollymook, NSW, Australia (BMNH 20030390; shell H = 14.6 mm). (C,D) *Austrolittorina unifasciata*, Mollymook, NSW, Australia (BMNH 20030393; shell H = 10.5 mm). (E,F) *Austrolittorina antipodum*, Wellington Harbour, New Zealand (BMNH 20030394; shell H = 8.8 mm). (G,H) *Austrolittorina cincta*, Bethels Beach, Auckland, New Zealand (BMNH 20030395; shell H = 12.0 mm). Scale bars = 50 µm.

- Nodilittorina pyramidalis*.—Abbott, 1954: 451, 456 (in part; includes *Echinolittorina trochoides*). McMichael, 1959: 27. Iredale & McMichael, 1962: 38. Macpherson & Gabriel, 1962: 90, fig. 119 (in part; includes *E. trochoides*). Wilson & Gillett, 1971: 30 (in part; pl. 11, fig. 11, 11a are *E. trochoides*). Wilson & Gillett, 1979: 52 (in part; pl. 8, fig. 3 is *E. trochoides*; pl. 8, fig. 3a is *E. australis* [Gray, 1826]). Jansen, 1995: 31, fig. 95; Reid, 1998: 739, fig. 15.100B, E (oviduct). Reid, 2002b: figs. 1A, 2B (penis). Williams *et al.*, 2003.
- Nodilittorina (Nodilittorina) pyramidalis pyramidalis*.—Rosewater, 1970: 424, 481–484, pl. 325, figs. 24, 25, pl. 370, figs. 1, 2, 6, 7, pl. 372 (distribution) (in part; other figures are *E. trochoides*).
- Nodilittorina (Nodilittorina) pyramidalis*.—Reid, 1989: 100, pl. 2, fig. 2i, figs. 7k (penis), 10j (oviduct), 14l (radula). Wilson, 1993: 147 (in part; pl. 18, fig. 5a,b are *E. trochoides*).
- Littorina (Tectarius) nodulosa*.—Weinkauff, 1882: 43–44, pl. 5, figs. 5–6 (not *Trochus nodulosus* Gmelin, 1791 = *E. trochoides*). Weinkauff, 1883: 225 (as *Tectaria*; not Gmelin, 1791).
- Tectarius nodulosus*.—Tryon, 1887: 258, pl. 48, fig. 72 (not Gmelin, 1791; in part; includes *Echinolittorina tuberculata*, *E. trochoides*, *Tectarius antonii*).
- Littorina nodulosa*.—Etheridge, 1889: 24 (not Gmelin, 1791).
- Tectaria nodulosa*.—Tate & May, 1901: 389 (not Gmelin, 1791).
- Nodilittorina nodulosa*.—Fischer, 1967: 47–80 (not Gmelin, 1791; in part; includes *E. trochoides*). Fischer, 1969: 119–129 (not Gmelin, 1791; in part; includes *E. trochoides*).
- Tectarius tuberculatus*.—Iredale, 1924: 243–244 (not *Littorina tuberculata* Menke, 1828 = *Echinolittorina tuberculata*).
- Nodilittorina tuberculata*.—Allan, 1950: 80, textfig. 19: 7 (not Menke, 1828). Macpherson & Chapple, 1951: 118 (not Menke, 1828).

Taxonomic history. This species has a complex taxonomic history, as a result of the longstanding confusion of at least six littorinid species that have superficially similar nodulose shells. Gmelin (1791) based his *Trochus nodulosus* on two figures in Chemnitz (1781: pl. 163, figs. 1545, 1546) of shells obtained by Captain Cook in the South Seas. These have been interpreted as examples of the present species (Weinkauff, 1882), which does indeed occur at Cook's landing place in Botany Bay (Iredale, 1924). However, if the figure is an accurate representation, the tall spire with small white nodules, nodulose base, narrow columella and rounded anterior lip, together leave little doubt that the species is that now identified as *Echinolittorina trochoides* (see Remarks below), which could well have been obtained during Cook's itinerary further north in Australia. Most subsequent authors failed to discriminate between *N. pyramidalis*, endemic to southeastern Australia, and *E. trochoides*, widespread in Indo-Malaya, and used the same name for both. Following Weinkauff (1882), some adopted the name *nodulosa* (e.g., Tryon, 1887; Fischer, 1967), overlooking the fact that it was unavailable, being a junior primary homonym of *Trochus nodulosus* Solander, 1766. Iredale (1924) believed that the earliest available name was *Littorina tuberculata* Menke, 1828, but this is a western Atlantic species (included by Gmelin as variety "minor" of his *T. nodulosus*; see discussion by Abbott, 1954; Bandel & Kadolsky, 1982). The first available name for a nodulose, western Pacific species is *Littorina pyramidalis* Quoy & Gaimard, 1833 and this has been widely used in the literature.

At first, the epithet *pyramidalis* was correctly applied, to include only the present species (Philippi, 1846; Reeve, 1857; Angas, 1867; Nevill, 1885; von Martens, 1897), but from the end of the nineteenth century a broader species

concept began to prevail. Tryon (1887) considered that nodulose shells from the western Atlantic and western Pacific were indistinguishable and synonymized them as *Tectarius nodulosus*. Abbott (1954) used the name *Nodilittorina pyramidalis* for a supposed single species extending from India to Australia and the Far East (i.e. *N. pyramidalis* s.st. and *E. trochoides*). A similar concept was adopted by Fischer (1967, as *N. nodulosa*) and by Rosewater (1970, but with an additional subspecies *N. pyramidalis pascua* Rosewater, 1970, on Easter Island, now regarded as a distinct species of *Echinolittorina*). It is in this incorrect sense that the name *N. pyramidalis* has since been generally applied. Meanwhile, some Australian workers had correctly observed that two nodulose species occurred in eastern Australia. This was presumably the basis for the inclusion of both *Tectarius malaccanus* (Philippi, 1847) (= *E. trochoides*) and *T. nodulosus* (presumably *N. pyramidalis*) in Hedley's (1910) list of Queensland shells. Iredale & Allan (1940) and Endean *et al.* (1956) also remarked on the likely presence of two *Nodilittorina* species in eastern Australia, but without making any taxonomic recommendation. Nevertheless, it was only in 1989 that both *N. pyramidalis* and *N. trochoides* appeared in the list of worldwide Littorinidae (Reid, 1989; updated by Reid, 2002b) and the latter was formally redescribed by Reid (1992, 2002a). Although some of its characters have been illustrated in phylogenetic studies (Reid, 1986, 1989, 2002b; also Reid, 1998), the present account is the first full description of *N. pyramidalis*.

From the original figure, without locality or details, *Littorina duplicata* Deshayes, 1850 appears superficially similar to *N. pyramidalis*; however, it is a fossil species probably belonging to the family Amberleyidae (based on examination of non-type specimens labelled *Littorina duplicata* in MNHN).

Diagnosis. Shell large; two rows of prominent nodules on last whorl, nodules not axially aligned, no nodules on base; blue-grey; aperture brown with two cream bands. Penis with numerous minute mamilliform glands in swollen filament; single large mamilliform gland on base, but no distinct glandular disc. Pallial oviduct with two consecutive loops of egg groove, in albumen and capsule glands; copulatory bursa opens near anterior end of pallial oviduct.

Material examined. 94 lots (56 AMS, 9 USNM, 24 BMNH, 2 IRSNB, 2 ZMA, 1 NMW), including 18 penes, 4 sperm samples, 6 pallial oviducts, 3 radulae.

Shell (Fig. 2). Mature shell height 8.6–26.8 mm. Shape high-turbinate to conical ($H/B = 1.23\text{--}1.46$; $SH = 1.59\text{--}2.02$); shoulder of spire whorls with single row of pointed nodules; single row of nodules on shoulder and another at periphery of final whorl; moderately solid. Columella short, broad, excavated, slightly flared or projecting as a rounded lip anteriorly; eroded parietal area present. Sculpture of fine raised spiral threads over entire surface, 19–25 on final whorl, separated by grooves equal in width to threads, threads weaker towards centre of base; spiral microstriae cover surface, but are frequently eroded; two rows of prominent pointed nodules at shoulder and periphery of final whorl, each 12–25, but not strictly aligned along axial (prosocline) growth lines; axial growth lines prominent, closely spaced, becoming lamellose towards end of final whorl, with no consistent relation to nodules. Protoconch

not well preserved, but about 0.4 mm diameter and about 3 whorls. Colour blue-grey, darker where eroded, with whitish nodules; aperture dark brown with two cream bands (corresponding with base and shoulder of whorl).

Animal. Head and sides of foot grey to black; tentacle with two broad (sometimes indistinct) black stripes, sometimes fused to become almost entirely black, pale at tip. Opercular ratio 0.54–0.63. Penis (Fig. 3A–E): filament relatively short, 0.3–0.5 total length of penis, slightly pointed and usually swollen, sometimes reddish, no constriction differentiating filament from wrinkled base, filament bears numerous papillae (structurally, these are miniature mamilliform penial glands, with mucous reservoir and subepithelial glandular tissue; Reid, 1989); sperm groove open to tip; single large mamilliform gland in short lateral projection of base, surrounded by subepithelial glandular tissue homologous with penial glandular disc (but not separated as a distinct glandular flap, and sometimes only visible by histology); penis unpigmented; penis reduced in size from April to June, but not shed (Underwood, 1974). Euspermatozoa 117–123 μm ; paraspermatozoa (Fig. 3I,J) are clusters of large spherical granules, 15–25 μm diameter, sometimes with short wedge-shaped or elongate rod bodies visible. Pallial oviduct (Fig. 3F–H) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, opaque pink, within which portion adjacent to egg groove (translucent capsule gland) is differentiated as a ring, reddish when fresh; copulatory bursa confined to straight section of pallial oviduct, opening near anterior end.

Spawn and development. Not recorded, but protoconch and large capsule gland indicate pelagic spawn and planktotrophic development; from condition of ovary, spawning at a maximum in January and February (Underwood, 1974).

Radula (Fig. 4A,B). Relative radular length 2.3–4.0. Rachidian: length/width 1.25–1.80; major cusp elongate, rounded or pointed at tip. Lateral and inner marginal: major cusps large, elongate, bluntly rounded at tip. Outer marginal: 6–7 cusps.

Habitat. This species is common in the littoral fringe of rocky shores; it is the dominant mollusc above high water of spring tides, extending higher where splash and spray permit (Endean *et al.*, 1956) and exceptionally up to 12 m above sea level (Dakin *et al.*, 1948). It thus extends to higher levels than the sympatric *Austrolittorina unifasciata*, and occurs at lower densities (to 32 m^{-2} at Cape Banks, NSW; Branch & Branch, 1981). It occurs mainly on ocean coasts and is said to be more common on shores of moderate to high exposure to waves (Endean *et al.*, 1956), although it can sometimes be found on moderately sheltered shores in inlets and harbours. Quantitative study has failed to find a consistent correlation between density and wave exposure near Sydney (Chapman, 1995a). On a small scale, the highest densities are associated with microhabitats of deep crevices, cracks and pits, whereas few occur on open rock surfaces (Chapman, 1994b). Although largely restricted to the top of the shore, animals occur sporadically on the upper mid-shore, where pits and topographic irregularities allow (Chapman, 1994b). Small specimens have been reported lower on the shore than adults (Johnston, 1917) and are scarce, so that recruitment appears sparse and probably

occurs mainly within pits in the rock (Underwood, 1974; Chapman, 1994b; Chapman & Underwood, 1994). Dispersion and behaviour have been studied (Chapman & Underwood, 1994; Chapman, 1999).

Range (Fig. 5). Eastern Australia, from easternmost Victoria to southern Queensland; Lord Howe Island and Norfolk Island. The only record from Victoria is from Mallacoota (37°33'S 149°47'E, AMS C50368; Bennett & Pope, 1953; Macpherson & Gabriel, 1962). The species is abundant along the entire length of the rocky coastline of New South Wales, and is also frequent in southern Queensland as far north as Noosa Heads (26°23'S 153°09'E, AMS C386700). Further north *N. pyramidalis* has been recorded from only four localities: Urangan, Hervey Bay (25°17'S 152°54'E, AMS C386710), Bustard Bay (24°05'S 151°48'E, AMS C62608), North Keppel Island (23°04'S 150°54'E, AMS C386762 plus 3 more lots) and Ocean Heads, Yeppoon (23°8.5'S 150°46'E, AMS C386768 plus 2 more lots). This species occurs at Lord Howe Island (AMS C089673; BMNH 1925.5.7.1; USNM 684715; Iredale & Allan, 1940), but is said to be “not common” (Etheridge, 1889, as *Littorina nodulosa*). There is a single old record from Norfolk Island (AMS C059382, A. Bell, 1910–1911).

Remarks. The shell does not show conspicuous variation (Fig. 2). Statistically, there are significant differences in shape between shores, but this is not correlated with wave exposure, overall size or population density (Chapman, 1995a). On one pair of shores at Cape Banks the shell aperture and foot were larger on the wave-exposed shore than on the more sheltered one, but it is not known if this is a general pattern (Chapman, 1997).

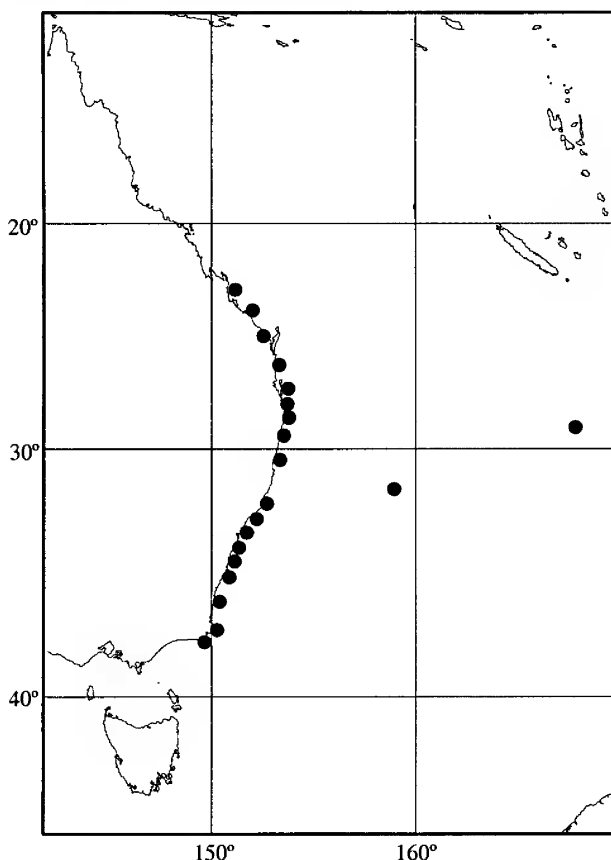


Fig. 5. Distribution of *Nodilittorina pyramidalis*.

Table 2. Characters useful for the discrimination of *Nodilittorina pyramidalis* and *Echinolittorina trochoides*.

character	<i>Nodilittorina pyramidalis</i>	<i>Echinolittorina trochoides</i>
geographical range	Yeppoon, Queensland to Mallacoota, Victoria	tropical Australia south to Hervey Bay; elsewhere Indo-Malaya to Japan
shell		
height	8–27 mm	6–18 mm
shape	broader (H/B 1.23–1.46)	narrower (H/B = 1.49–1.72)
nodules	1 row of nodules on penultimate whorl	usually 2 rows of nodules on penultimate whorl
basal sculpture	cords not nodulose	cords usually bear small nodules
apertural shape	slightly flared and angled at base of columella	anterior edge more rounded
colour	blue-grey with white nodules	grey-brown with cream nodules
apertural colour	brown with 2 cream bands	brown with single basal cream band
penis		
filament	many papillae (minute mamilliform glands) on swollen filament	no papillae on smoothly tapering filament
base	no discrete glandular disc adjacent to large mamilliform gland	glandular disc adjacent to large mamilliform gland
pallial oviduct		
egg groove	egg groove makes large circular loop in capsule gland	no loop in capsule gland
copulatory bursa	simple sac	bursa divides into two branches

The distributions of *N. pyramidalis* and the conchologically similar *Echinolittorina trochoides* are almost mutually exclusive in eastern Australia. The former is characteristic of the eastern overlap zone (Ponder & Wells, 1998), whereas the latter is a widespread tropical species. Based on a survey of the distribution of common intertidal organisms along the Queensland coast, Endean *et al.* (1956) placed the biogeographic boundary between shores of northern (tropical) and southern (temperate) character at 25°S (Hervey Bay). This is also the southernmost record of *E. trochoides* (AMS C386753, Point Vernon, Hervey Bay, 25°15'S 152°49'E). These two species have been recorded together at only two localities: Bustard Bay (24°05'S 151°48'E; although in two separate lots: *N. pyramidalis* AMS C62608; *E. trochoides* AMS C386794) and the Keppel Islands (23°04'S 150°54'E; three formerly mixed lots of the two species in AMS now separated and registered as: C106933 plus 386781, C089660 plus 386787, C386762 plus 386780, numbers of *N. pyramidalis* plus *E. trochoides* in these lots are: 31 plus 2, 60 plus 1, 54 plus 33, respectively). Endean *et al.* (1956) pointed out that this faunistic boundary was not correlated with temperature change and suggested that exposure to wave action was critical. South of 25°S the coast is exposed to strong surf and oceanic swells, whereas to the north it is largely sheltered by the Great Barrier Reef. Presumably other hydrographic factors, such as nutrients and productivity, are also connected with the contrast between oceanic and reef-sheltered coasts. The distribution of *N. pyramidalis* and *E. trochoides* north of 25°S does correlate to some extent with wave-exposure. Bustard Bay (where both have been recorded) is semi-exposed (Endean *et al.*, 1956), whereas in the shelter of nearby Port Curtis only *E. trochoides* has been found. Yeppoon (and presumably the adjacent Keppel Islands) is an exposed

locality (Endean *et al.*, 1956). Nevertheless, in the southern parts of its range *E. trochoides* does occur in both exposed and sheltered localities. The seven collections of *N. pyramidalis* from Yeppoon and the Keppel Islands in AMS are not all precisely dated, but five are pre-1950 and two no later than 1966; it is not known whether this species can still be found there.

The discrimination of *N. pyramidalis* and *E. trochoides* is usually straightforward (Table 2). Their geographical ranges barely overlap and anatomical features are diagnostic. In females, the loop of the egg groove through the capsule gland is present only in *N. pyramidalis*, whereas a forked copulatory bursa is unique to *E. trochoides* (Reid, 1992: fig. 2i). In males, papillae on the penial filament and lack of a discrete glandular disc distinguish *N. pyramidalis* (cf. *E. trochoides*, Reid, 1992: fig. 1j; Reid, 2002b: fig. 2E). The larger, broader shell and produced anterior lip of *N. pyramidalis* are the most useful conchological characters, but small shells can be difficult to separate. In the northern parts of its range the shells of *N. pyramidalis* are smaller; those from Queensland rarely exceed 18 mm and in the three sympatric samples of *N. pyramidalis* and *E. trochoides* the largest of the 145 specimens of *N. pyramidalis* is only 14.8 mm. In these mixed samples the two species are mainly of similar size and separation requires careful examination of aperture shape, coloration and sculpture (Table 2; for *E. trochoides* see Reid, 1992: pl. 3a–c; Reid, 2001: fig. 2G, H). The largest shells of *N. pyramidalis* are found on Lord Howe Island, where sizes of greater than 23 mm are common.

The phylogenetic relationships of *Nodilittorina pyramidalis* remain unclear. In a recent analysis of DNA-sequence data from two nuclear and two mitochondrial genes, Williams *et al.* (2003) showed only that it was a member of a large clade including the genera *Tectarius*,

Austrolittorina, *Cenchritis* and *Littoraria*. Within this group, the most likely (but still weakly supported) positions were at the base of the clade, or as the sister-group of *Tectarius*. This latter possibility is intriguing, for it is supported by the unique feature of papillae on the penial filament, shared by *N. pyramidalis* and the subgenera *Tectarius*, *Tectininus* and *Echininus* of *Tectarius* (but not the subgenera *Liralittorina* or *Echininiopsis*). Other features such as the form of the outer marginal radular teeth and the loop of the egg groove within the capsule gland, which had been interpreted as evidence for a relationship with *Austrolittorina* (Reid, 2002b) are now known to be convergent (Williams *et al.*, 2003).

Austrolittorina Rosewater, 1970

Littorina (*Austrolittorina*) Rosewater, 1970: 467 (type *Littorina unifasciata* Gray, 1826, by original designation).

Taxonomic history. This generic name was introduced as a subgenus of *Littorina* (implicitly by reason of the smooth, spirally striate shell of its members, see Taxonomic History of *Nodilittorina*, above). In the original diagnosis, Rosewater (1970) mentioned a “predominantly southern ocean and tropical distribution”, “flattened columella and crescent-shaped area on the adjacent part of the shell” (i.e. the eroded parietal area), and a penis with single penial gland and penial glandular disc (in terminology of Reid, 1989; i.e. penis of the type characteristic of *Nodilittorina s.l.*). No unique features were identified by which to define the group and, in addition to the species here included, at least nine others (belonging to *Echinolittorina*, *Afrolittorina* and *Littoraria* in current classification) were listed. Three further species were added subsequently (Ponder & Rosewater, 1979). As discussed above, with new insights into the anatomy of littorinids the definition of *Nodilittorina* was broadened and *Austrolittorina* placed in its synonymy (Bandel & Kadolsky, 1982; Reid, 1989). The name was not used again until Reid (2002a) provisionally employed it as a subgenus of *Nodilittorina*, to denote eight or nine Southern Ocean species united by a loop of the egg groove within the capsule gland of the pallial oviduct (*N. araucana* was not then recognized as belonging to this group). Formal phylogenetic analysis of the morphological characters of *Nodilittorina s.l.* failed to confirm these ten southern species as a clade, and as a result no taxonomic decisions were made (Reid, 2002b).

In a recent molecular study, all ten of these southern littorinines were included and the five species here included in *Austrolittorina* appeared as a strongly supported clade; the name was therefore used at the rank of genus for the first time, and a formal diagnosis given (Williams *et al.*, 2003). Of the morphological characters listed in the following diagnosis, none is unique. One that is, however, distinctive is the absence of axial colour markings (i.e. axial lines, or axially aligned series of spots or dashes) that characterize the majority of littorinine species. Shells are not always of the bluish-white appearance of the type species, *A. unifasciata*; *A. araucana* may be brown or whitish and *A. cincta* typically has spiral brown lines.

Diagnosis. Shell not nodulose; spiral striae or smooth; eroded parietal area; no pseudoubilicus; white with peripheral blue-grey band, brown, or with spiral brown lines; no axial colour pattern. Cephalic tentacles black. Penis with

swollen filament; base bifurcate; single mamilliform gland adjacent to glandular disc of subepithelial glandular tissue; penial vas deferens an open groove. Paraspermatozoa with short, curved or coiled rod bodies, or rod bodies absent. In pallial oviduct egg groove makes a simple loop through albumen gland, circular loop (or only slight flexure) through capsule gland, no loop in jelly gland; copulatory bursa opens in anterior or posterior position. (After Williams *et al.*, 2003.)

Austrolittorina unifasciata (Gray, 1826)

Figs. 4C,D, 6–8, 25A,B

Littorina unifasciata Gray, 1826: 483 (Australia; restricted to King George Sound, Western Australia (Rosewater, 1970); lectotype (Rosewater, 1970) BMNH 1968373/1 (fig. 6A) plus 1 paralectotype BMNH 1968373/2, seen). Angas, 1865: 172. Tenison Woods, 1878: 36. Guiler, 1958: 139. Haacke, 1885: 504–505 (in part, includes *Afrolittorina praetermissa*). Wilson & Gillett, 1979: 52, pl. 8, fig. 6, 6a.

Littorina unifasciata.—Menke, 1844: 57.

Melarhaphé unifasciata.—Iredale, 1915: 447 (in part; includes *A. antipodum*). Hedley, 1916: 186 (as *Melarhaphé*). Hedley, 1918: M51. May, 1921: 48. May, 1923: 49, pl. 22, fig. 19. Cotton & Godfrey, 1938: 10. Macpherson & Chapple, 1951: 118 (as *Melarhaphé*). Kershaw, 1955: 307 (as *Melarhaphé*). Wilson & Gillett, 1971: 30, pl. 11, fig. 12, 12a (as *Melarhaphé*).

Melarapha unifasciata.—McMichael, 1959: 27. Macpherson & Gabriel, 1962: 87, fig. 115.

Littorina (*Austrolittorina*) *unifasciata*.—Rosewater, 1970: 423, 467–470, pl. 325, figs. 17–18, 326, fig. 5, pl. 359, figs. 1–5, pl. 360, figs. 1–4, pl. 361, figs. A (radula), C (penis), pl. 362 (distribution).

Nodilittorina (*Nodilittorina*) *unifasciata*.—Bandel & Kadolsky, 1982: 37.

Littorina (*Austrolittorina*) *unifasciata*.—Ludbrook & Gowlett-Holmes, 1989: 564, fig. 11.19j, k. Wilson, 1993: 146–147, pl. 18, fig. 3.

Nodilittorina (*Nodilittorina*) *unifasciata*.—Reid, 1989: 100, pl. 2, fig. 2j.

Nodilittorina unifasciata.—Jansen, 1995: 31, fig. 94. Reid, 1998: 739, fig. 15.100D (penis). Reid, 2002b: fig. 1c.

Nodilittorina (*Austrolittorina*) *unifasciata*.—Reid, 2002a: 154.

Austrolittorina unifasciata.—Williams *et al.*, 2003.

Littorina diemenensis Quoy & Gaimard, 1833: 479–480; pl. 33, figs. 8–10 (la partie sud de la Nouvelle-Hollande, de l'île de Van-Diemen et même de la Nouvelle-Zélande [southern Australia, Tasmania and New Zealand]; restricted to Tasmania (Rosewater, 1970); lectotype (Rosewater, 1970) MNHNP 10.2x5.9 mm plus 11 dry paralectotypes plus 11 dry paralectotypes plus 82 alcohol paralectotypes plus 39 alcohol paralectotypes, all MNHNP, seen; in part; from locality New Zealand, includes *L. antipodum*). Deshayes, 1843: 209. Reeve, 1858: *Littorina* sp. 94, pl. 17, fig. 94. Nevill, 1885: 141.

Littorina (*Melarhaphé*) *diemenensis*.—Adams & Adams, 1854: 314 (as *Melarhaphé*).

Melarapha diemenensis.—Iredale & McMichael, 1962: 38.

Littorina acuta Menke, 1843: 9 (Western Australia; types presumed lost; synonymized with *Littorina unifasciata* Gray, 1826, by Menke, 1844).

Littorina mauritiana.—Philippi, 1847: 165; *Littorina* pl. 3, fig. 17a (not *Phasianella mauritiana* Lamarck, 1822 = *Littoraria mauritiana*; in part; figs. 15 and 17b are *Echinolittorina ziczac* (Gmelin, 1791), also includes *Littoraria mauritiana*). Weinkauff, 1882: 97–98 (not Lamarck, 1822; pl. 14, fig. 4 is *E. ziczac*; also includes *L. mauritiana*). Weinkauff, 1883: 220 (not Lamarck, 1882; in part; includes *L. mauritiana*). Watson, 1886: 574 (not Lamarck, 1822; in part; includes *L. mauritiana*). Verco, 1908: 8 (not Lamarck, 1822). Hedley, 1910: 355.

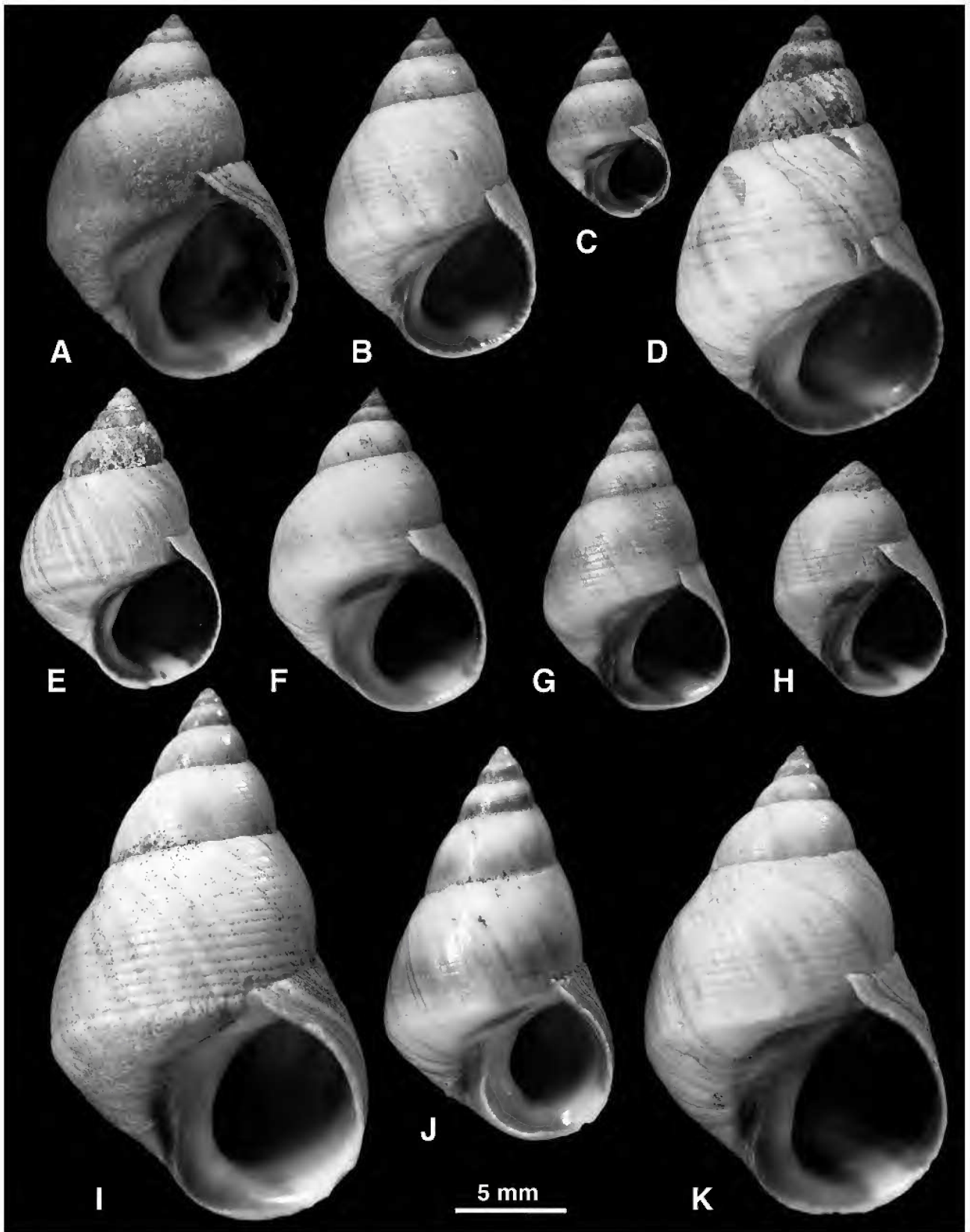


Fig. 6. *Austrolittorina unifasciata*: (A), lectotype of *Littorina unifasciata* Gray, 1826; no locality (BMNH 1968373/1). (B,D) Mollymook, NSW, Australia (BMNH 20030396). (C) Stony Point, Western Port Bay, Victoria, Australia (BMNH 20030397). (E) Fairlight, Sydney, NSW, Australia (BMNH 20030398). (F,G) Trigg Island, WA, Australia (BMNH 20030399). (H) Bucroft Head, Jervis Bay, NSW, Australia (BMNH 1925.4.1.16). (I–K) Lord Howe Island (AMS C059516).

- Littorina mauritiana*.—Reeve, 1858: *Littorina* sp. 100 (not Lamarck, 1822; in part; fig. 100 is *Echinolittorina ziczac* (Gmelin, 1791), also includes *Littoraria mauritiana*). Angas, 1867: 209 (not Lamarck, 1822; in part; includes *Littoraria mauritiana*). Smith, 1884: 60–61 (not Lamarck, 1822; in part; includes *Austrolittorina antipodum*). Gatliff, 1887: 60 (not Lamarck, 1822). Tate & May, 1901: 389 (in part; includes *Afrolittorina praetermissa*). Pritchard & Gatliff, 1902: 909–91 (not Lamarck, 1822; in part; includes *Littoraria mauritiana*, *A. antipodum*).
- Littorina (Melarhapha) mauritiana*.—Tryon, 1887: 247, pl. 44, figs. 72, 73, 75 (as *Melarapha*; not Lamarck, 1822; in part; figs. 70, 74 are *A. cincta*; fig. 71 is *E. ziczac*; also includes *A. antipodum*, *L. mauritiana*).
- Littorina diemenensis* var. *mauritiana*.—Etheridge, 1889: 24 (not Lamarck, 1822).
- Melarhapha mauritiana*.—Iredale, 1912: 223 (not Lamarck, 1822).
- Littorina diemensis* Philippi, 1847: 195, 196, *Littorina* pl. 4, fig. 1 (unjustified emendation of *Littorina diemenensis* Quoy & Gaimard, 1833, because original spelling is quoted, and emended spelling is used twice and in index; in part; includes *Austrolittorina antipodum*). Küster, 1856: 18, pl. 2, figs. 23–24 (in part; includes *A. antipodum*). Weinkauff, 1878: 31. Weinkauff, 1883: 218 (in part; includes *A. antipodum*, *A. cincta*, *Echinolittorina novaezelandiae* [Reeve, 1857]).
- Littorina mauritiana* var. *crassior* Philippi, 1847: 165; *Littorina* pl. 3, figs. 15, 17a [Cuba (fig. 15); other localities mentioned (not specifically for var. *crassior*) are Mauritius; Nova Hollandia (Australia); Ducee's Island (Ducie Island); restricted to Australia (Rosewater, 1970); lectotype (here designated) Philippi, 1847: fig. 17 (left; 17a in text); in part; fig. 15 is said to come from Cuba and therefore probably *Echinolittorina ziczac* (Gmelin, 1791), probably also includes *Littoraria mauritiana* (Lamarck, 1822)].
- Littorina africana*.—Reeve, 1857: *Littorina* sp. 37, pl. 8, figs. 37a,b (not Krauss, in Philippi, 1847; in part; includes *Afrolittorina africana*).
- Littorina laevis*.—Reeve, 1858: *Littorina* sp. 95, pl. 17, fig. 95 (not Philippi, 1846 = *Littoraria mauritiana*).
- Littorina caerulescens*.—Tenison Woods, 1879: 65–72 (as *coerulescens*; not *Turbo caerulescens* Lamarck, 1822 = *Melarhapha neritoides* (Linnaeus, 1758); in part; includes *A. antipodum*, *Afrolittorina praetermissa*, *A. africana*, *Littoraria mauritiana*, *L. undulata* (Gray, 1839), *M. neritoides*).
- Littorina diemenensis* var. *pseudolaevis* Nevill, 1885: 141 (New South Wales; Port Jackson [Sydney Harbour, New South Wales]; types in ZSI, not seen).

Taxonomic history. This species has a complex taxonomic history, owing to longstanding confusion with several littorinids with similar smooth, white shells. Although the species was first described by Gray in 1826, for the rest of the century the name *Littorina unifasciata* was generally considered a junior synonym of *Littorina mauritiana*. The misidentification of the present species as *L. mauritiana* originated with Philippi (1847), who was deceived by Lamarck's (1822) inadequate description of *Phasianella mauritiana* and by Delessert's (1841) poor figure of one of Lamarck's shells, which does indeed resemble *A. unifasciata*. The species described by Lamarck (1822) is an endemic of Mauritius and the southwestern Indian Ocean, as correctly recognized by Nevill (1885; see Rosewater, 1970, for detailed discussion and lectotype designation), and now classified as a species of *Littoraria* (Reid, 1986). Philippi's (1847) concept of *Littorina mauritiana* may not have included actual specimens of *Littoraria mauritiana* (although he did refer to Delessert's figure), because he had himself described that species as *Littorina laevis* Philippi, 1846, from an unknown locality, and figured it accurately in his monograph (Philippi, 1847: *Littorina* pl. 6, fig. 6). Nevertheless, his concept did not

include *A. unifasciata* alone. He recognized two named varieties, *Littorina mauritiana* var. *crassior* and var. *gracilior*. One of the two figures of var. *crassior* (fig. 17a) is a typical shell of *A. unifasciata*, but the other (fig. 15) was said to come from Cuba. The latter figure is indeterminate, but if the locality is correct then it can only be *Echinolittorina ziczac*. Philippi's var. *gracilior* was illustrated by a single figure (fig. 17b); the original shell from the Cuming Collection has been discovered in the BMNH and is undoubtedly a specimen of *E. ziczac*, distinguished by its elongate shape, almost smooth surface and two white bands within the aperture. Shells of *E. ziczac* with the normal zigzag pattern are distinctive, but occasional white shells such as this one do bear a superficial resemblance to *A. unifasciata*. An incomplete accompanying label in Philippi's hand bears the name "*L. mauritiana* from the Isle of Jua—". This is interpreted as "Juan Fernández", and the two other specimens in the syntypic series are probably *A. fernandezensis* (distinction from *A. unifasciata* based on shells alone is sometimes impossible). It appears, then, that Philippi based his *L. mauritiana* var. *gracilior* on a mixture of *E. ziczac* and *A. fernandezensis*, both of which are indeed usually more elongate than typical *A. unifasciata*. It is curious that neither the locality nor Cuming are mentioned by Philippi in his brief remark on var. *gracilior*. However, among the localities for *Littorina mauritiana* he lists "insula Ducee's in Oc. Pacifico (Cuming)". This is a reference to Ducie Island in Polynesia, where none of these species occurs. Conceivably, Philippi may have confused the two Pacific localities of Ducie Island and the Juan Fernández Islands. Following Philippi's (1847) misuse of the name *L. mauritiana*, the name was generally applied to the Australian species and *unifasciata* only returned to common use after the differences between the species of Gray and Lamarck were pointed out by Iredale (1915).

Austrolittorina unifasciata has also sometimes been known by the name *Littorina diemenensis* Quoy & Gaimard, 1833. These authors described their species from Australia, l'île de Van-Diëmen (i.e. Tasmania) and New Zealand, and therefore must have included not only *A. unifasciata* but also *A. antipodum*, for only the latter occurs in New Zealand. However, all known type specimens are *A. unifasciata*, in agreement with the type locality that was restricted to Tasmania by Rosewater (1970). Philippi (1847) accepted *L. diemenensis* as a distinct species (and was followed by Küster, 1856; Weinkauff, 1878, 1883), but distinguished it from his concept of *L. mauritiana* only by its smaller size. Philippi also described a still smaller species, found only in New Zealand, as *Littorina antipodum*. Nevertheless, confusion between *A. unifasciata* and *A. antipodum* continued and the two were considered conspecific by several subsequent authors (see Taxonomic History of *A. antipodum*).

The white-shelled, mainly large, Southern Hemisphere littorinids have often been combined as a single species. Tenison Woods (1879) first expressed this view, and in its most extreme form, combining *A. unifasciata*, *A. antipodum*, *Afrolittorina praetermissa*, *Afrolittorina africana*, *Littoraria mauritiana* and even the European *Melarhapha neritoides* into a single taxon for which he used the name *Littorina caerulescens* (= *M. neritoides*). This choice of name was justified by quoting Deshayes (1843), although in fact the quote was from Quoy & Gaimard (1833), who compared their *L. diemenensis* with *L. caerulescens* and concluded that they were distinct. Tryon (1887) also had a broad concept, including *A. unifasciata*, *A. antipodum*, *A. cincta*

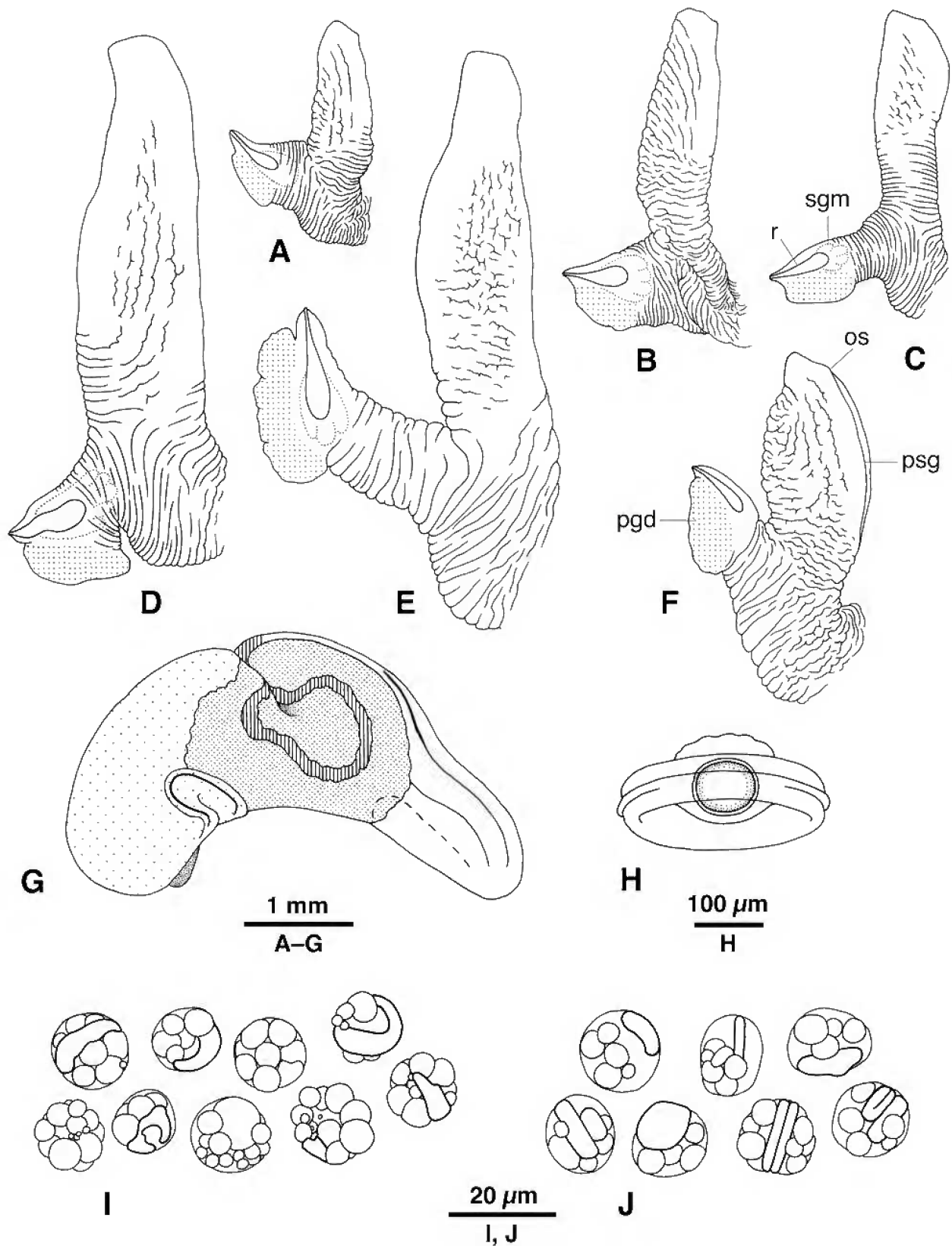


Fig. 7. *Austrolittorina unifasciata*: (A–F) Penes. (G) Pallial oviduct. (H) Egg capsule (after Rudman, 1996). (I, J) Paraspermatozoa from two specimens. (A, B, I) Blackmans Bay, Tasmania, Australia (BMNH 20030401). (C) Nongarrup, Albany, Western Australia (BMNH 20030402). (D) Lord Howe Island (AMS C356440). (E) Thompson Memorial Park, Lord Howe Island (BMNH 20030403). (F, J) North Harbour, Sydney, NSW, Australia (BMNH 20030404). (G) Mollymook, NSW, Australia (BMNH 20030393). (H) Harbord, Sydney, NSW, Australia. Shell heights: (A) 6.6 mm, (B) 6.7 mm, (C) 9.7 mm, (D) 15.7 mm, (E) 20.0 mm, (F) unknown, (G) 10.5 mm. Abbreviations: (os) subterminal opening of penial sperm groove; (pgd) penial glandular disc (subepithelial glandular material visible by transparency); (psg) penial sperm groove; (r) receptacle of mamilliform penial gland (visible by transparency); (sgm) subepithelial glandular material of mamilliform penial gland (visible by transparency). Shading conventions as in Fig. 3.

and *Littoraria mauritiana* under the name *Littorina mauritiana*. In his monograph of the Indo-Pacific members of the family, Rosewater (1970) recognized three subspecies of *Littorina unifasciata*, the typical one from Australia, subsp. *antipodum* from New Zealand, and subsp. *fernandezensis* from the Juan Fernández Islands. Kilburn (1972) went further, suggesting that *Afrolittorina africana* was probably an additional subspecies of this supposed circumpolar taxon. Only in 1989 were these taxa all listed as distinct species, although without formal redescription (Reid, 1989).

The types of Nevill's var. *pseudolaevis* have not been examined, but he cited Reeve's (1858) fig. 95, which is *L. unifasciata*.

Bandel & Kadolsky (1982) included *Littorina cubana* Weinkauff, 1882 in the synonymy of *L. unifasciata*, citing the spiral sculpture and lack of colour markings, and accordingly corrected its type locality to Australia. However, the original description also mentioned a turreted spire and two pale bands within a brown aperture; these features are never seen in *L. unifasciata*, and unequivocally identify this species as *Echinolittorina ziczac*. This western Atlantic species does occasionally show spiral striae and absence of colour pattern, and it occurs in Cuba. The original figure of Weinkauff (1882: pl. 9, figs. 2–3) is unrecognizable, and types are presumed lost, but the author cited plate 3, figure 17 of Philippi (1847), which is of *L. unifasciata* and *E. ziczac*, as discussed above.

Diagnosis. Shell moderately large; sculpture of spiral striae; white with indistinct broad band of blue-grey above periphery. Penis with broad, wrinkled filament; glandular disc and mamilliform gland on base. Pallial oviduct with two consecutive loops of egg groove, in albumen and capsule glands.

Material examined. 167 lots (108 AMS, 31 USNM, 19 BMNH, 2 IRSNB, 3 ZMA, 2 MNHNP, 2 NMW), including 18 penes, 7 sperm samples, 7 pallial oviducts, 4 radulae.

Shell (Fig. 6, 25A,B). Mature shell height 3 (Nwe, 1974) to 24.9 mm. Shape turbate to tall-spined ($H/B = 1.23\text{--}1.83$; $SH = 1.25\text{--}2.16$); spire outline straight to slightly convex; whorls gently rounded, suture slightly impressed, periphery slightly angled; solid. Columella pillar slightly concave; columella slightly excavated; eroded parietal area present; outer lip of aperture usually minutely lirate just within margin. Sculpture of 10–12 primary spiral grooves above periphery, that remain as equidistant incised lines throughout growth of shell, continuing faintly on base, occasionally becoming obsolete on final whorl; strong spiral microstriae cover surface; surface, especially spire, often eroded; growth lines weak. Protoconch rarely preserved, 0.36 mm diameter, 3 whorls. Colour white with a more or less distinct broad band of blue-grey above periphery; apex brownish, second and third whorls of teleoconch marked by 5–9 fine spiral brown lines on grey ground (Fig. 25A,B), but lined pattern always disappears on larger shells; aperture dark brown with basal white band.

Animal. Head and sides of foot black; tentacles grey to black, usually with indistinct transverse lines, sometimes a paler longitudinal streak, unpigmented around eye only. Opercular ratio 0.37–0.53. Penis (Fig. 7A–F): filament approximately 0.6–0.7 total length of penis, but not distinctly demarcated from wrinkled base, broad, sometimes

swollen, bluntly pointed, surface with reticulate wrinkles (in life and preserved); sperm groove opens subterminally; single large, often narrow, mamilliform gland and adjacent flap of penial glandular disc borne together on lateral branch of base; penis unpigmented; penis does not show annual regression (Nwe, 1974; Underwood, 1974). Euspermatozoa 61–69 μm ; paraspermatozoa (Fig. 7I,J) are spherical clusters of large spherical granules, 13–17 μm diameter, usually with 1–2 rod bodies of short cylindrical or arcuate or irregular shape (occasionally indistinct or possibly absent), not projecting from cell. Pallial oviduct (Fig. 7G) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, opaque pink, within which portion adjacent to egg groove (translucent capsule gland) is differentiated as a ring; copulatory bursa confined to straight section of pallial oviduct, opening near anterior end.

Spawn and development. Spawn (Fig. 7H) a transparent pelagic capsule 240 μm diameter containing a single ovum 100 μm diameter, capsule with roughened dome surrounded by circumferential skirt with median ridge described from Sydney by Rudman (1996); smaller capsules 100–140 μm , with ovum 80 μm , described from vicinity of Adelaide by Nwe (1974); development planktotrophic; breeding throughout the year near Adelaide (Nwe, 1974); year-round recruitment recorded in Tasmania (Chen & Richardson, 1987); females mature from October to May at Cape Banks (NSW) with peak spawning from December to March (Underwood, 1974).

Radula (Fig. 4C,D). Relative radular length 3.5–4.8. Rachidian: length/width 1.21–1.62; major cusp elongate, rounded at tip. Lateral and inner marginal: major cusps large, elongate, bluntly rounded at tip or rectangular. Outer marginal: 6–8 cusps.

Habitat. This species is ubiquitous and abundant on most of the temperate shores of Australia and has been included in numerous ecological surveys and field experiments. It can be found on any hard substrate, including schist, granite, sedimentary rock, concrete and even wooden piers (Nwe, 1974). On exposed coasts it is abundant in the littoral fringe up to the highest level of spring tides (reaching higher levels with stronger wave action) and in the upper barnacle zone, whereas juveniles are present at lower levels among barnacles and *Pyura* (Dakin *et al.*, 1948; Guiler, 1951; Bennett & Pope, 1953, 1960; Underwood, 1981; Wells, 1984; Chen & Richardson, 1987). On sheltered shores it extends lower, almost to low water of neap tides (Endean *et al.*, 1956), but is absent from sites of extreme shelter (Guiler, 1952a; Womersley & Edmonds, 1958; Branch & Branch, 1981). Densities can be remarkably high on shores of moderate exposure (to 9600 m^{-2} at Cape Banks, NSW), resulting in extreme intraspecific competition for food (Branch & Branch, 1981). On a small scale, the species shows a patchy distribution both within and between shores, but some trends have been identified: snails are largest in the upper and lowermost parts of the tidal range, and density is negatively correlated with size; animals are clustered in pits and crevices, and are more common on horizontal surfaces and where barnacles are present; there is no relation between density and exposure of the shore (Britton *et al.*, 1991; Chapman, 1994a; Underwood & Chapman, 1996). The food consists of microalgae, sporelings and lichens (Branch & Branch, 1981; Jernakoff, 1983). Detailed studies of

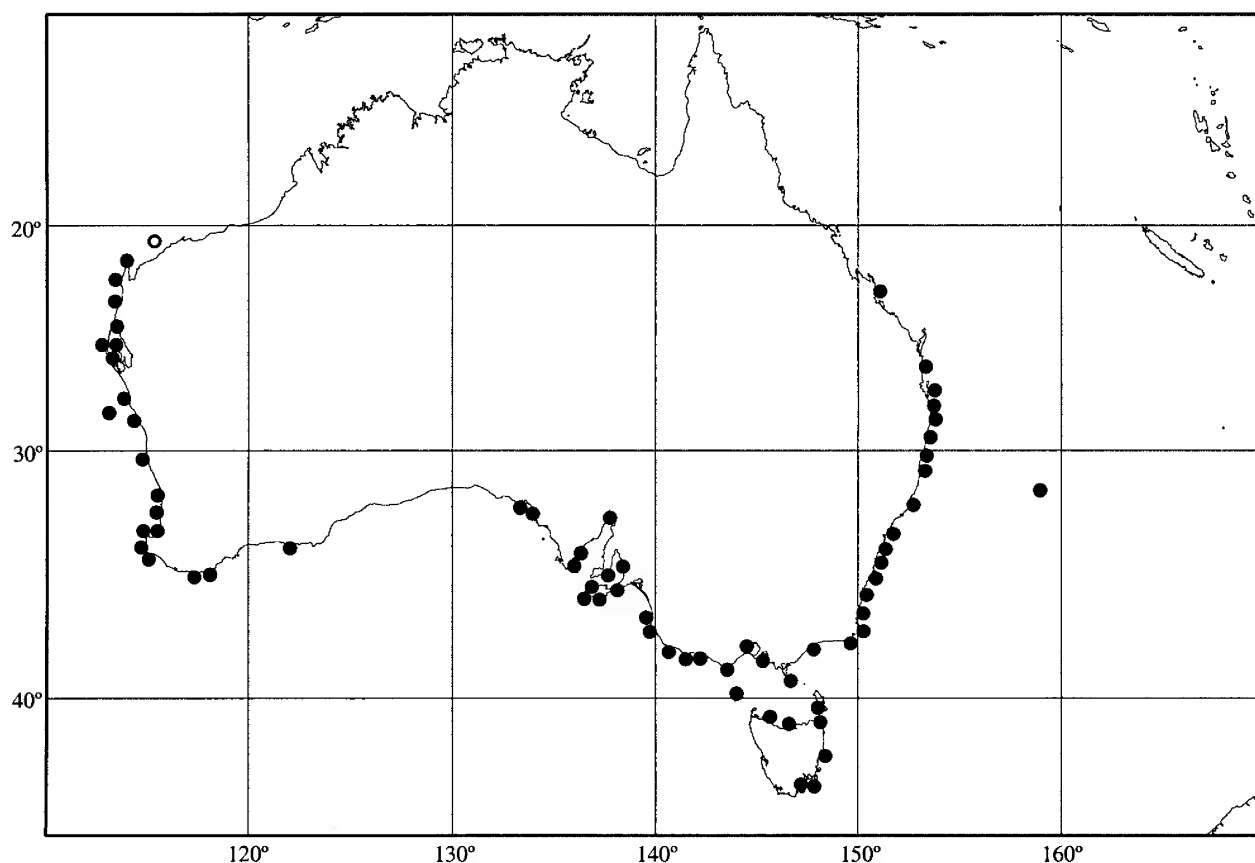


Fig. 8. Distribution of *Austrolittorina unifasciata*. Open circle is a record from F.E. Wells (pers. comm.).

movement (Underwood & Chapman, 1985, 1989), foraging (Chapman, 2000), behaviour following transplant (Chapman, 1986, 1999), dispersion in relation to microtopography (Underwood & Chapman, 1989, 1992) and aggregation behaviour (Chapman, 1995b, 1998; Chapman & Underwood, 1996) have been done in New South Wales. Over its extensive geographical range, it is microsympatric with *N. pyramidalis* in New South Wales and southern Queensland (but that species extends higher in the littoral fringe), with *Afrolittorina praetermissa* in Victoria, Tasmania and South Australia (but that species occurs at lower levels, in more cryptic habitats, and is common on more sheltered shores), and with *Echinolittorina australis* (Gray, 1826) in Western Australia.

Range (Fig. 8). Temperate and subtropical coastline of Australia, Tasmania and Lord Howe Island. In Western Australia there are numerous records as far north as North West Cape (21°45'S 114°10'E, AMS C387269), which was given as the northwestern limit of this species by Wells (1980), and a single specimen from Barrow Island is present in WAM (F.E. Wells, pers. comm.). There is a record from still further north at Cape Keraudren (19°57'S 119°45'E, coll. F. Haddrill, 1976, AMS C389557), but this is considered doubtful (F.E. Wells, pers. comm.). A lot from Vansittart Bay in the far north of WA (Coll. W. Burrows, AMS C45183) is certainly unreliable (this may perhaps be the source of the northwestern extralimital record on the distribution map by Rosewater, 1970: pl. 362). There are no records from the Great Australian Bight between the Archipelago of the Recherche, WA (34°15'S 112°50'E, AMS C69337) and Point Sinclair, SA (32°06'S 133°00'E, AMS C387947), but this is probably a collecting artefact resulting

from the inaccessibility of this coastline. Further east there are abundant records from the coastlines of South Australia, Victoria, Tasmania and New South Wales, as far north as Point Cartwright and Noosa Heads in southern Queensland (26°23'S 153°09'E, AMS C386963, C107999). Endean *et al.* (1956) noted that the northern limit in Queensland was associated with wave action; at Noosa and southwards the species was abundant on exposed shores, but to the north it was replaced on sheltered shores by *Echinolittorina vidua* (Gould, 1859) (as *Melarhapha melanacme*). Only a single reliable lot has been seen from further north, at Yeppoon (23°08'S 158°44'E, 6 specimens, collected in 1952, AMS C387974), and this is also an exposed locality; to the north the coast is sheltered by the Great Barrier Reef. Rosewater (1970: pl. 362) plotted a record in the vicinity of Cooktown, but gave no details in the text and this record is considered unreliable. The species is common on Lord Howe Island (5 lots AMS, 3 lots BMNH), where shells reach unusually large size, and there is a single record from Elizabeth Reef (29°56'S 159°04'E, USNM 767443, not seen). In Tasmania it is common on the east coast and islands of Bass Strait, sporadic on the sheltered north coast and in the south, but is absent from the exposed west coast (Bennett & Pope, 1960; contrary to Kershaw, 1958, who may have confused the species with *Afrolittorina praetermissa*). Whether this absence from western Tasmania is a consequence of the strong exposure, or of the low sea temperatures produced by the cold current of the West Wind Drift, is not known.

Remarks. The size and shape of the shell show significant variation (Fig. 6). Size gradients on the shore have been mentioned above; adult size has been said to be larger in

either sheltered (Nwe, 1974) or exposed sites (Branch & Branch, 1981), but no consistent correlation of size with wave-exposure was found in a well-replicated survey of shores at Cape Banks, New South Wales (Chapman, 1994a). As in many littorinids, sexual dimorphism has been reported, the males being smaller (Nwe, 1974). An early study at a single site reported a relatively larger shell aperture on the exposed side of a wall (Bassingthwaighe & Foulds, 1985), but although supported by at least one comparison between shores of contrasting exposure (Chapman, 1997), this may not be a general pattern (McMahon, 1992). Indeed, Chapman (1995a) emphasized that variation in shape within shores was as great as that between shores, and found no consistent correlations with density, size or exposure; the only consistent pattern was a decrease in relative aperture size at higher levels on the shore. Functional interpretations of intraspecific variation in littoral gastropods have suggested that tall shells with small apertures contain and conserve larger reserves of water, that these are more resistant to crushing by predators, and that enlarged apertures improve tenacity when wave action is strong. However, experimental tests failed to support these suggestions for *A. unifasciata* (Chapman, 1997). The planktrophic mode of larval development implies high gene flow within and between nearby shores, so it is likely that the differences described are the result of phenotypic plasticity rather than genotypic adaptation (McMahon, 1992; Chapman, 1995a). One possibility is a direct effect of growth rate (determined by time available for feeding) on shell shape; slower growth at high levels on the shore might produce the more elongate form (Chapman, 1997).

This well-known species is unlikely to be confused with any of the littorinids with which it is sympatric. Shells of *A. fernandezensis*, endemic to the Juan Fernández and Desventuradas Islands off Chile, are so similar that they are sometimes indistinguishable; usually they are slightly more elongate than *A. unifasciata* and the margin of the aperture is more distinctly lirate. Shells of *A. antipodum*, found in New Zealand, are smaller, more tall-spined and have a more pronounced bluish peripheral band (see Remarks on *A. antipodum*). The penes of all three species are diagnostic.

The molecular analysis of Williams *et al.* (2003) showed that the sister species of *A. unifasciata* is *A. fernandezensis*. The authors explained this interesting trans-Pacific relationship as a case of dispersal from Australia to the east, because the estimated age of the divergence (13–30 million years) was later than the breakup of Gondwana that might have provided a vicariant explanation. They did, however, point out that the distance across the Pacific is too great for larval dispersal under the present-day current regime, so that it may have been accomplished by use of formerly emergent seamounts as stepping stones.

Austrolittorina fernandezensis (Rosewater, 1970)

?*Littorina mauritiana* var. *gracilior* Philippi, 1847: 165 (no locality in text; 3 syntypes BMNH 20020038 plus 20020039; in part; 2 syntypes probably this species, but largest syntype, figured by Philippi, 1847: *Littorina* pl. 3, fig. 17b, is *Echinolittorina ziczac*).

Littorina (*Austrolittorina*) *unifasciata fernandezensis* Rosewater, 1970: 471–472, pl. 359, figs. 9–12, pl. 361, fig. B (radula), pl. 363 (distribution) (east shore of Cumberland Bay, Isla Más a

Tierra, Juan Fernández Islands [Chile]; holotype USNM 368900, Rosewater, 1970, pl. 359, figs. 11–12, seen; 25 paratypes USNM 679256, seen; 11 paratypes DMNH 039221, not seen).

Nodilittorina (*Austrolittorina*) *fernandezensis* Reid, 2002a: 151–154, figs. 18Q–V, 20 (distribution), 21G–J (penes), L (pallial oviduct), O, P (paraspermatozoa), 22C, D (radula).

Austrolittorina fernandezensis.—Williams *et al.*, 2003.

Taxonomic history. For full synonymy, see Reid (2002a). As discussed above (see Taxonomic History of *A. unifasciata*) the name *Littorina mauritiana* var. *gracilior* Philippi, 1847 was probably partly based on this species, although this is speculative. To exclude this name from the synonymy of *A. fernandezensis*, the largest figured syntype (BMNH 20020038), which is undoubtedly a specimen of *E. ziczac*, is here designated lectotype.

Diagnosis. Shell large; spiral sculpture of fine microstriae; aperture finely lirate; white with broad indistinct blue-grey zone above periphery. Penial filament small, pointed; small mamilliform gland and large glandular disc on base. Pallial oviduct with two consecutive loops of egg groove, in albumen and capsule glands.

Range. Juan Fernández Islands and Desventuradas Islands, southeastern Pacific Ocean.

Remarks. See Remarks on *A. unifasciata* for distinction from that species.

Austrolittorina antipodum (Philippi, 1847)

Figs. 4E,F, 9–11

Littorina diemenensis Quoy & Gaimard, 1833: 479–480 (in part; not *L. diemenensis* Quoy & Gaimard, 1833 = *A. unifasciata*). Reeve, 1858: *Littorina* sp. pl. 17, fig. 94 (not Quoy & Gaimard, 1833). Hutton, 1878: 27 (not Quoy & Gaimard, 1833).

Littorina diemensis.—Philippi, 1847: 195, *Littorina* pl. 4, fig. 1 (not *L. diemensis* Philippi, 1847, emendation of *Littorina diemenensis* Quoy & Gaimard, 1833 = *A. unifasciata*; in part; includes *A. unifasciata*). Weinkauff, 1883: 218 (in part; includes *A. unifasciata*, *A. cincta*, *Echinolittorina novaezelandiae*).

Littorina antipodum Philippi, 1847: 195–196, *Littorina* pl. 4, fig. 2 (New Zealand; lectotype, here designated, Philippi, 1847: *Littorina* pl. 4, fig. 2; fig. 9D herein). Weinkauff, 1882: 61–62, pl. 8, fig. 4. *Littorina* (*Melarhaphe*) *antipodum*.—Adams & Adams, 1854: 314 (as *Melaraphe*).

Littorina antipodum.—Nevill, 1885: 143.

Littorina (*Austrolittorina*) *unifasciata antipodum*.—Rosewater, 1970: 423 (as *antipoda*), 470–471, pl. 359, figs. 6–8, pl. 360, fig. 5, pl. 362 (distribution). Powell, 1976: 87, pl. 16, fig. 12. Powell, 1979: 87, pl. 23, fig. 9.

Nodilittorina (*Nodilittorina*) *antipodum*.—Reid, 1989: 99.

Nodilittorina antipodum.—Spencer & Willan, 1996: 18.

Nodilittorina (*Austrolittorina*) *antipodum*.—Reid, 2002a: 154.

Austrolittorina antipodum.—Williams *et al.*, 2003.

Littorina caerulea.—Tenison Woods, 1879: 65–72 (as *coerulea*; not *Turbo caerulea* Lamarck, 1822 = *Melarhaphe neritoides*; in part; includes *A. unifasciata*, *Afrolittorina praetermissa*, *A. africana*, *Littoraria mauritiana*, *M. neritoides*). Hutton, 1880: 79 (not Lamarck, 1822; in part; includes *A. unifasciata*). Hutton, 1882: 164, pl. 7, fig. E (radula; not Lamarck, 1822).

Littorina mauritiana.—Smith, 1884: 60–61 (not *Phasianella mauritiana* Lamarck, 1822 = *Littoraria mauritiana*; in part; includes *A. unifasciata*). Suter, 1901: 214 (not Lamarck, 1822).

Iredale, 1910: 70–71 (not Lamarck, 1822).

Littorina (Melarhaphe) mauritiana.—Tryon, 1887: 247 (as *Melaraphe*; not Lamarck, 1822; includes *A. unifasciata*, *A. cincta*, *L. mauritiana*, *Echinolittorina ziczac*).

Littorina (Melarhaphe) mauritiana.—Suter, 1913: 188, pl. 38, fig. 28 (not Lamarck, 1822; includes *A. unifasciata*, *L. mauritiana*; as *Melaraphe*; as *Littorina mauritiana* in Atlas, 1915).

Littorina mauritiana.—Bucknill, 1924: 37, pl. 7, fig. 22.

Melarhaphe unifasciata.—Iredale, 1915: 447 (not *Littorina unifasciata* Gray, 1826 = *A. unifasciata*; in part; includes *A. unifasciata*). Oliver, 1915: 518 (not Gray, 1826).

Melarhaphe zelandiae.—Finlay, 1928: 241 (not Finlay, 1927 = *A. cincta*).

Melarhaphe oliveri Finlay, 1930: 224–225 (Hampden, east coast of South Island, New Zealand; holotype Auckland Museum AK 70456 (formerly TM456) plus 1 paratype AK 72574 (formerly TM456), not seen). Powell, 1937: 67, pl. 9, fig. 12. Powell, 1962: 83, pl. 9, fig. 12 (as *Melarhapha*). Morton, 1975: fig. 6a–c (radula), fig. 7a,b (stomach).

Melarapha oliveri.—Dell, 1963: 225.

Taxonomic history. There has been a long history of inclusion of this species as a single taxon with the Australian *A. unifasciata*, and sometimes also with other superficially similar white-shelled littorinids (see Taxonomic History of *A. unifasciata*). Quoy & Gaimard (1833) listed the locality New Zealand for their species *L. diemenensis* and therefore evidently considered the Australian and New Zealand species to be the same (although the name has now been restricted to *A. unifasciata*). This concept was followed by Philippi (1847), although in addition he introduced *Littorina antipodum* for smaller, taller-spined, less markedly striated shells with a dark peripheral band, found in New Zealand. This name was almost entirely neglected for 120 years (exceptions were Weinkauff, 1882; Nevill, 1885), until used as a subspecies of *L. unifasciata* by Rosewater (1970). Instead, the species was generally combined with *A. unifasciata* under the name *L. mauritiana* (Smith, 1884; Suter, 1901, 1913; Iredale, 1910; Bucknill, 1924). Following Iredale (1915), the name *Melarhaphe unifasciata* was briefly used in New Zealand (Oliver, 1915). Iredale (1915) had also suggested that “the Neozelanic shell may prove subspecifically separable”, which induced Finlay (1927) to introduce the new name *M. zelandiae*. However, as Finlay (1930) later confessed: “Owing ... to a curious and unpardonable misconception of species I described the wrong shell” (the description applied to the other New Zealand littorinid, *A. cincta*). He therefore introduced yet another name, *M. oliveri*, for the present species, which was widely used in New Zealand (e.g., Powell, 1937, 1962; Dell, 1963). This was superseded by the older name *L. unifasciata antipodum* following the revision by Rosewater (1970). The taxon was given full specific status in the worldwide family list of Reid (1989), although the anatomical evidence justifying this decision was not presented. Rudman (1996) noted that the differences between the egg capsules of *A. unifasciata* and *A. antipodum* supported separate species status for both.

No type specimens of *Littorina antipodum* are known to exist, and to obviate any further confusion as to the identity of the taxon Philippi's (1847) figure is here designated lectotype. The shape and coloration of the shell leave no doubt as to its identity (Fig. 9D). The specific epithet is a noun in the genitive case, not an adjective that should agree in gender with the feminine generic name (e.g., Rudman, 1996).

It may be noted that *Littorina novaezelandiae* Reeve, 1857 was mistakenly said to come from New Zealand in its original description; it is a valid species of *Echinolittorina* that is endemic to Sri Lanka (Reid, 2001).

Diagnosis. Shell small, usually tall-spined, often smooth; white with broad band of blue-grey above periphery. Penis with smooth, slightly swollen filament; glandular disc and mamilliform gland on base. Pallial oviduct with two consecutive loops of egg groove, in albumen and capsule glands.

Material examined. 76 lots (15 AMS, 18 USNM, 14 BMNH, 4 IRSNB, 4 ZMA, 1 MNHNP, 1 NMW, 19 MNZ), including 11 penes, 5 sperm samples, 7 pallial oviducts, 3 radulae.

Shell (Fig. 9). Mature shell height 5.4–13.7 mm. Shape high-turbinate to tall-spined (H/B = 1.36–2.20; SH = 1.43–2.63, exceptionally 3.22); spire outline straight to slightly convex; whorls gently rounded, suture slightly impressed, periphery slightly angled; solid. Columella pillar short, slightly concave; columella slightly excavated; small eroded parietal area sometimes present. Sculpture of 9–12 approximately equidistant primary spiral grooves (incised lines) may be present above periphery, continuing faintly on base, but frequently surface is almost smooth; microstriae absent; surface, especially spire, often eroded; growth lines weak. Protoconch rarely preserved, about 3 whorls, 375–425 µm length, sculptured by spiral rows of minute tubercles (Pilkington, 1971). Colour white, with broad spiral blue-grey band above periphery; rarely grey-black with white base, or almost entirely white with faint grey band; small juveniles entirely black or brown, with spiral white line on base; aperture dark brown with basal white band.

Animal. Head, tentacles and sides of foot black. Opercular ratio 0.47–0.61. Penis (Fig. 10A–E): filament 0.5 total length of penis, smooth, bluntly pointed, slightly swollen, sperm groove opens slightly subterminally; single large, often narrow, mamilliform gland and adjacent large flap of penial glandular disc borne together on short lateral branch of base; penial base often with black pigment. Euspermatozoa 75–82 µm; paraspermatozoa (Fig. 10H,I) spherical, 11–14 µm diameter, containing large spherical granules and a curved, twisted or torus-shaped rod body. Pallial oviduct (Fig. 10F) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, within which portion adjacent to egg groove (translucent capsule gland) is differentiated as a ring; copulatory bursa confined to straight section of pallial oviduct, opening near anterior end.

Spawn and development. Spawn (Fig. 10G) a transparent pelagic capsule 200–250 µm diameter, containing a single ovum 80 µm diameter, capsule with hemispherical dome sculptured by 3 concentric rings, peripheral ridge and a basal circumferential flange; development planktotrophic, inferred planktonic life of 1–2 months; spawning season November to March (at Otago; Pilkington, 1971).

Radula (Fig. 4E,F). Relative radular length 2.0–2.5. Rachidian: length/width 1.13–1.33; major cusp elongate, rounded or slightly pointed at tip. Lateral and inner marginal: major cusps large, elongate, bluntly rounded at tip. Outer marginal: 6–7 cusps.

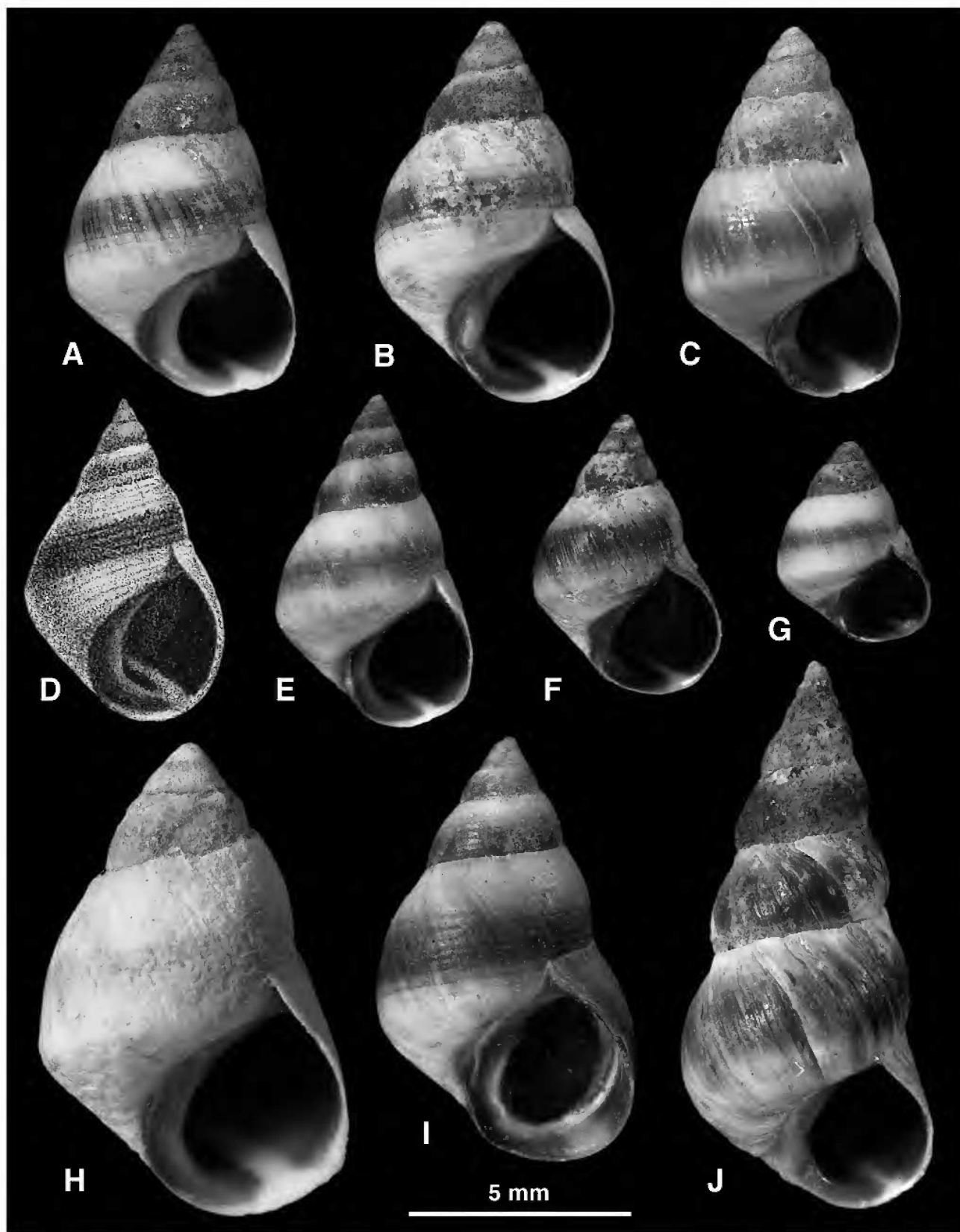


Fig. 9. *Austrolittorina antipodum*: (A) Auckland Harbour, New Zealand (BMNH 20030405). (B,F) Muriwai, New Zealand (BMNH 20030406). (C,E) Island Bay, Cook Strait, New Zealand (USNM 671202). (D) lectotype figure of *Litorina antipodum* Philippi, 1847 (Philippi, 1847: *Litorina* pl. 4, fig. 2). (G) Long Beach, Russell, New Zealand (BMNH 20030407). (H) Great Island, Three Kings Islands, New Zealand (MNZ M049237). (I) Raoul Island, Kermadec Islands (MNZ M214380). (J) Waitangi, Chatham Islands, New Zealand (MNZ M110492).

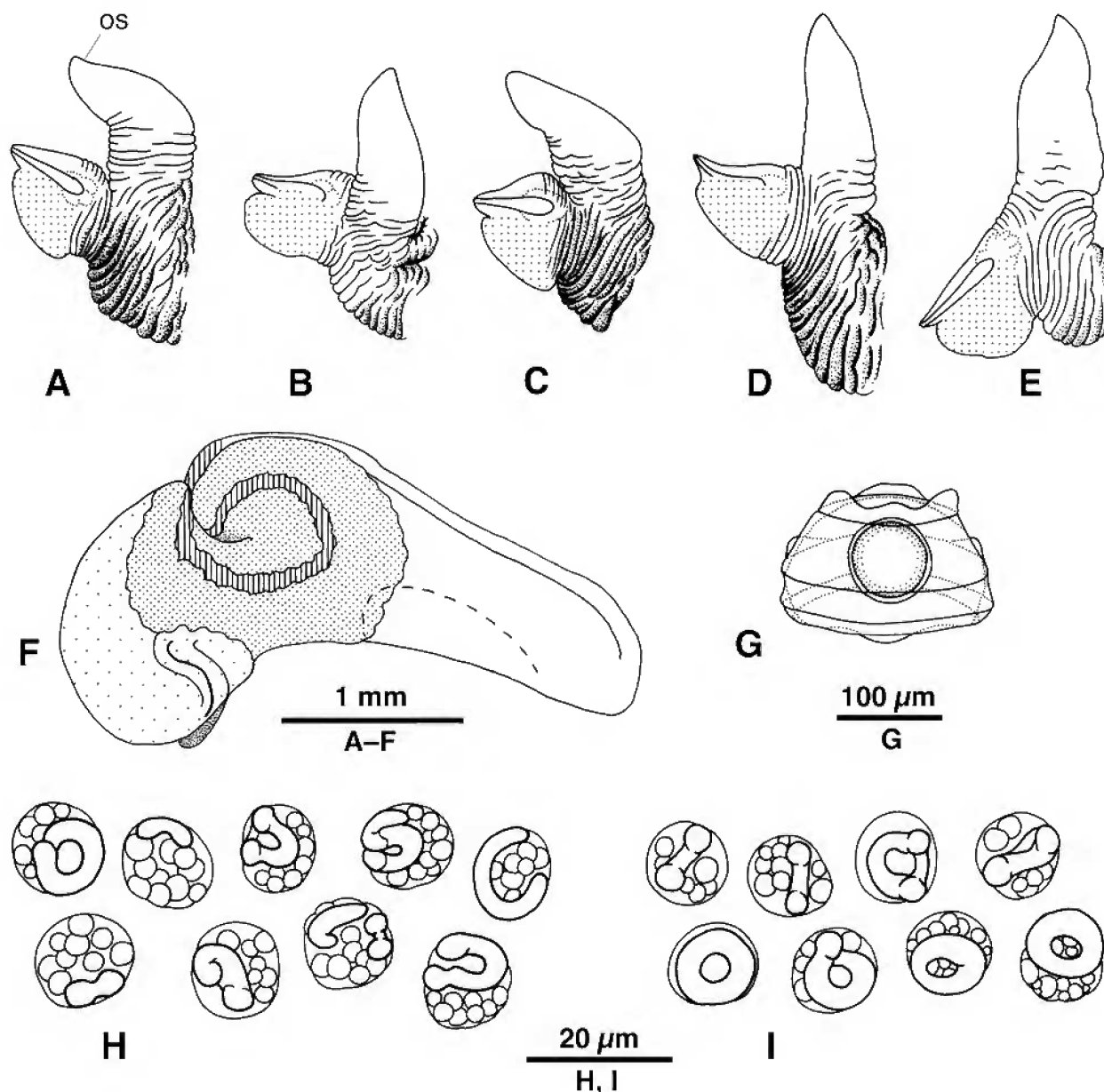


Fig. 10. *Austrolittorina antipodum*: (A–E) Penes. (F) Pallial oviduct. (G) Egg capsule (after Pilkington, 1971). (H, I) Paraspermatozoa from two specimens. (A–C, F, H) Wellington Harbour, New Zealand (BMNH 20030394). (D, E, I) Kaikoura, New Zealand (BMNH 20030408). (G) Portobello, Otago Harbour, New Zealand. Shell heights: (A) 7.5 mm, (B) 7.4 mm, (C) 7.4 mm, (D) 7.4 mm, (E) 8.9 mm, (F) 9.8 mm. Abbreviation: (os) subterminal opening of penial sperm groove. Shading conventions as in Fig. 3.

Habitat. Throughout much of New Zealand, especially in the north, this species is abundant on rocky shores from the top of the littoral fringe to the upper part of the barnacle zone (EHWST to MTL). Juveniles occur below adults, often among barnacles. The upper limit depends upon shade and spray, so that on the most strongly exposed, shaded vertical cliffs, it can reach 12 m above EHWST. It is less common on sheltered shores, scarce in extreme shelter, and absent where water is turbid. Shaded rock faces are favoured; on sunny faces, it occupies cracks and crevices and it may occur in shallow, high-level rock pools (Dellow, 1950; Knox, 1953; Foster, 1966; Morton & Miller, 1968). In the south of South Island *A. antipodum* is less common and occupies a more restricted vertical range, confined to the littoral fringe, and its distribution is shifted towards more sheltered

shores (Batham, 1956, 1958; Morton & Miller, 1968; Pilkington, 1971). At Rangitoto Island (near Auckland), it has been recorded among *Salicornia* and lava blocks on stiff mud (Powell, 1933a). The diet included black lichens, diatoms, *Ulva* and *Enteromorpha* (Powell, 1933a; Morton, 1975). It is frequently sympatric with *A. cincta* (see Habitat of *A. cincta* for comparison).

Range (Fig. 11). New Zealand, Chatham Islands, Kermadec Islands. This species occurs around the entire coastline of North and South Islands, and is also recorded from Stewart Island (Ringaringa, 46°44'S 168°09'E, MNZ M019600), Snares Islands (North Island, 48°02'S 166°36'E, MNZ M015474), Chatham Islands (Waitangi Bay, 43°57'S 176°33'W, MNZ M110471; Powell, 1933), Three Kings

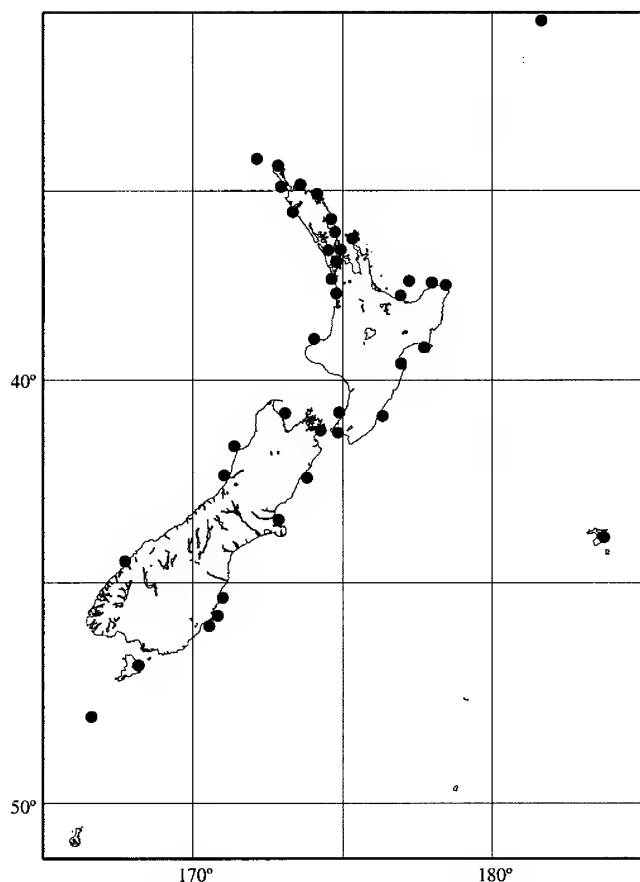


Fig. 11. Distribution of *Austrolittorina antipodum*.

Islands (Great Island, 34°09'S 172°09'E, MNZ 049237) and Kermadec Islands (Raoul Island, 29°16'S 177°55'W, MNZ M 214380, AMS). The species is reported to be rare in the Kermadec Islands (Iredale, 1910; Oliver, 1915; Brook, 1998); it is likely that only chance migrants reach these islands and that the population is not self-sustaining.

Remarks. Although superficially similar to the Australian *A. unifasciata*, these two species should not be confused. *Austrolittorina antipodum* is smaller, reaching only 13.7 mm in height (*A. unifasciata* attains 24.9 mm), more tall-spined, the spiral striae are less marked and often obsolete, microstriae are absent, the peripheral blue-grey band is more conspicuous, and the penial filament is shorter and not wrinkled. In addition, their ranges are allopatric. Throughout most of its range *A. antipodum* is sympatric with *A. cincta*, although it has a more northern distribution. The latter is readily separated by the brown spiral lines of its shell and larger size (to 20.2 mm); anatomically the two are similar, the penial filament of *A. cincta* being only slightly more pointed.

Occasionally shells of *A. antipodum* are found that are extremely elongate (H/B up to 2.21, SH up to 3.22; Fig. 9J); by analogy with other species (see Remarks on *Afrolittorina knysnaensis*) these probably represent specimens infected with trematode parasites, although this has not been confirmed by dissection.

Molecular data have shown that *A. antipodum* and *A. cincta* are sister species, with an estimated divergence time of more than 10 million years. Possible causes of this speciation are unknown; it is too recent to be ascribed to

the Oligocene transgression that greatly reduced the land area of New Zealand (Cooper & Millener, 1992). In turn, this pair is sister to the pair *A. unifasciata* plus *A. fernandezensis*, with a separation estimated as 23–44 million years (Williams *et al.*, 2003). This is younger than the attainment of the present width of the Tasman Sea, implying that dispersal took place from Australia to New Zealand.

Austrolittorina cincta (Quoy & Gaimard, 1833)

Figs. 4G,H, 12–14

Littorina cincta Quoy & Gaimard, 1833: 481–482, pl. 33, figs. 20–21 (New Zealand; lectotype (Rosewater, 1970) (fig. 12B) plus 2 paralectotypes, MNHNP, seen). Deshayes, 1843: 209–210. Reeve, 1857: *Littorina* sp. 53, pl. 11, fig. 53. Hutton, 1878: 27. Hutton, 1880: 78. Hutton, 1882: 164, pl. 7, fig. D (radula). Nevill, 1885: 143. Suter, 1901: 214–215.

Littorina cincta.—Philippi, 1847: 202, pl. 4, fig. 18. Weinkauff, 1882: 76, pl. 10, figs. 5, 8. Weinkauff, 1883: 222. Watson, 1886: 574. Bucknill, 1924: 37, pl. 7, fig. 23.

Littorina (Melarhapha) cincta.—Adams & Adams, 1854: 314 (as *Melarhapha*).

Littorina (Melarhapha) cincta.—Suter, 1913: 187, pl. 38, fig. 27 (as *Melarhapha*; as *Littorina cincta* in Atlas, 1915).

Melarhapha cincta.—Finlay, 1928: 241 (as *Malarhapha*). Powell, 1937: 67, pl. 9, fig. 13. Powell, 1955: 74. Powell, 1962: 83, pl. 9, fig. 13 (as *Melarhapha*). Dell, 1963: 225 (as *Melarhapha*).

Littorina (Austrolittorina) cincta.—Rosewater, 1970: 423, 473–474, pl. 364, figs. 1–6, pl. 365, fig. A (penis), pl. 366 (distribution). Powell, 1976: 87, pl. 16, fig. 13. Powell, 1979: 87, pl. 23, fig. 10.

Nodilittorina cincta.—Bandel & Kadolsky, 1982: 3. Spencer & Willan, 1996: 18.

Nodilittorina (Nodilittorina) cincta.—Reid, 1989: 99.

Nodilittorina (Austrolittorina) cincta.—Reid, 2002a: 154.

Austrolittorina cincta.—Williams *et al.*, 2003.

Littorina luctuosa Reeve, 1857: *Littorina* sp. 65, pl. 13, fig. 65 (New Zealand; 3 syntypes BMNH 1968315; Rosewater (1970: pl. 364, figs. 3, 4) figured one as “holotype”, but this is not a valid lectotype designation, ICZN, 1999: Arts 74.5, 74.6). Hutton, 1880: 79.

Littorina luctuosa.—Weinkauff, 1882: 72, pl. 9, fig. 12.

Littorina (Melarhapha) mauritiana.—Tryon, 1887: 247, pl. 44, figs. 70, 74 (as *Melarhapha*; not *Phasianella mauritiana* Lamarck, 1822 = *Littoraria mauritiana*; includes *A. unifasciata*, *A. antipodum*, *L. mauritiana*, *Echinolittorina ziczac*).

Melarhapha zelandiae Finlay, 1927: 375; pl. 18, figs. 18–19 (Dunedin Harbour, New Zealand; holotype Auckland Museum AK 70457 (formerly TM457) plus 3 paratypes AK 72526 (formerly TM457), not seen).

Taxonomic history. This species is readily recognized by its brown shell and has therefore been correctly identified by most authors. It was redescribed as *Littorina luctuosa* by Reeve (1857), a species incorrectly synonymized with *A. antipodum* (Weinkauff, 1883; Nevill, 1885) until its identity was indicated by Suter (1901, 1913). The species was inadvertently named again by Finlay (1927) as *M. zelandiae* (see Finlay, 1930; see Taxonomic History of *A. antipodum*). This species was included in a very broad concept of *L. mauritiana* by Tryon (1887; see Taxonomic History of *A. unifasciata*).

Diagnosis. Shell moderately large, usually tall-spined, sculptured with incised spiral lines; cream with brown spiral lines, or brown with pale grooves. Penis with bluntly pointed, slightly swollen filament; glandular disc and mamilliform gland on base. Pallial oviduct with two consecutive loops of egg

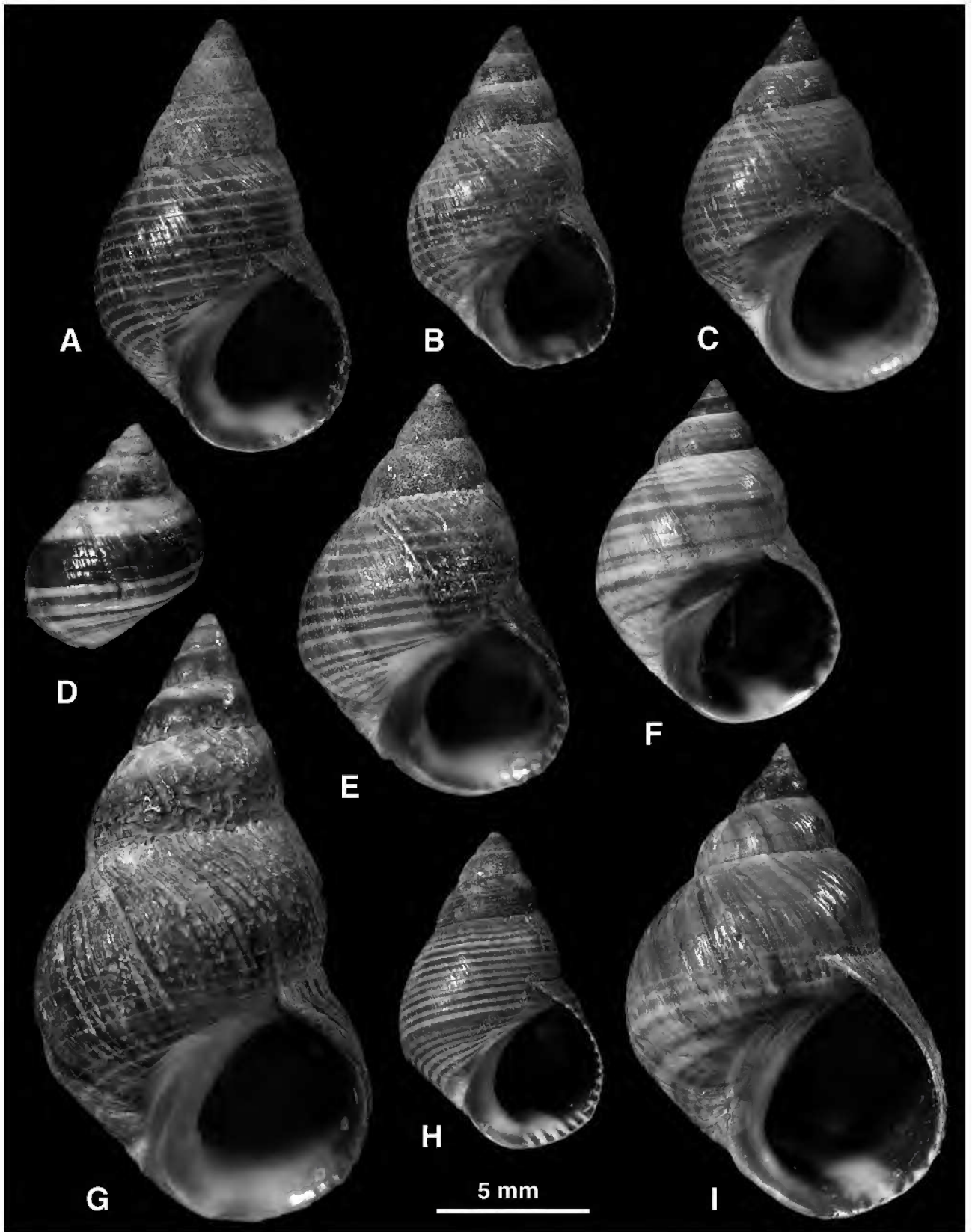


Fig. 12. *Austrolittorina cincta*: (A,E,H) Cyathea Cove, Tasman Bay, New Zealand (BMNH 20030409). (B) Lectotype of *Littorina cincta* Quoy & Gaimard, 1833 (MNHN unreg.). (C) Muriwai, New Zealand (BMNH 20030410). (D) Ringaringa, Stewart Island, New Zealand (MNZ M042428). (F) Flat Point, Wairarapa, New Zealand (MNZ M095414). (G) Port Waikato, New Zealand (BMNH 20030411). (I) New Zealand (BMNH 20030412).

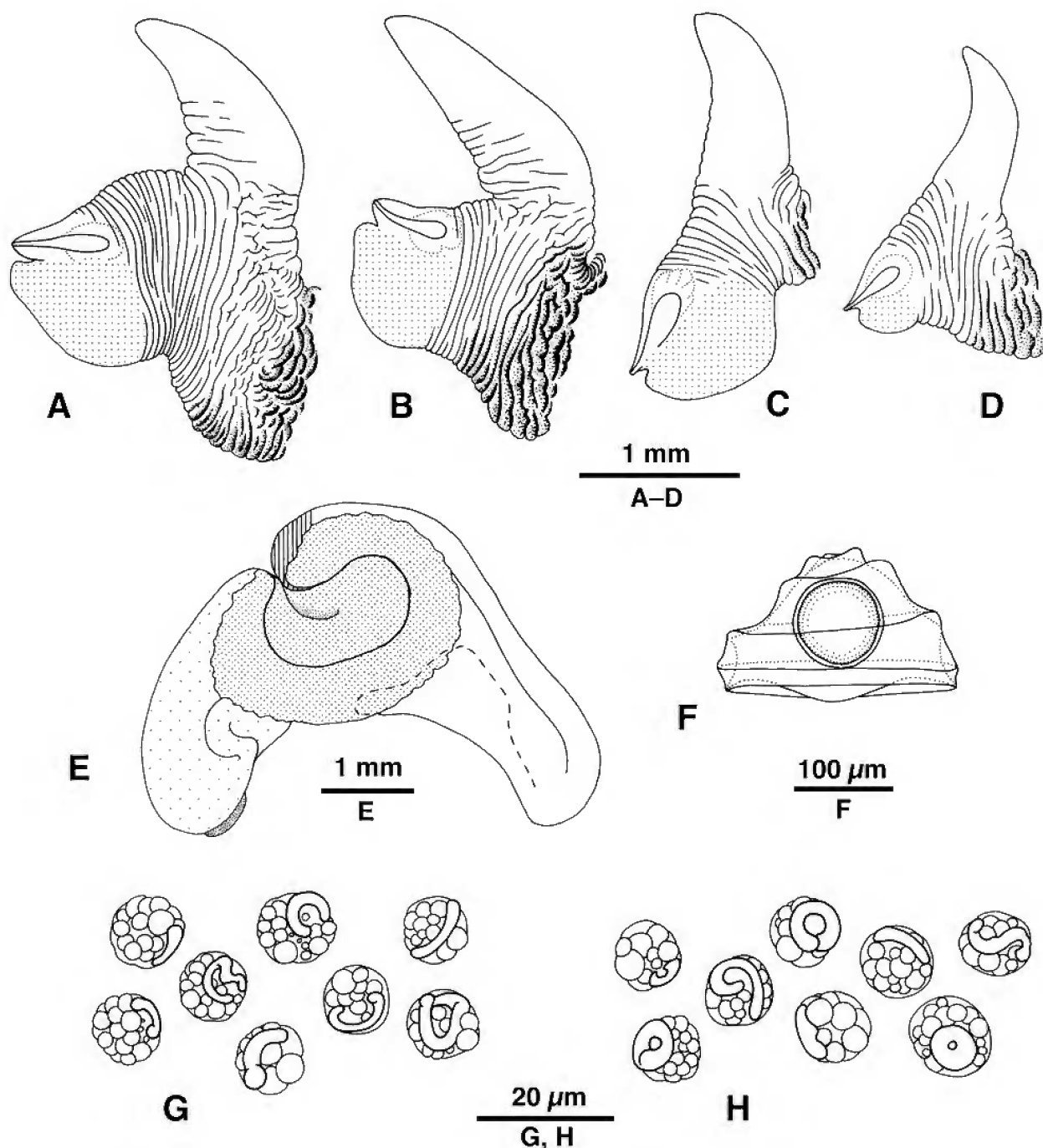


Fig. 13. *Austrolittorina cincta*: (A–D) Penes. (E) Pallial oviduct. (F) Egg capsule (after Pilkington, 1971). (G, H) Paraspermatozoa from two specimens. (A, E, G) Wellington Harbour, New Zealand (BMNH 20030413). (B, H) Kaikoura, New Zealand (BMNH 20030414). (F) Portobello, Otago Harbour, New Zealand. Shell heights: (A) 12.3 mm, (B) 10.4 mm, (C) 8.7 mm, (D) 8.9 mm, (E) 12.1 mm. Shading conventions as in Fig. 3.

groove, in albumen and capsule glands.

Material examined. 71 lots (17 AMS, 14 USNM, 13 BMNH, 2 IRSNB, 4 NMW, 21 MNZ), including 6 penes, 4 sperm samples, 4 pallial oviducts, 4 radulae.

Shell (Fig. 12). Mature shell height 8.9–20.2 mm. Shape high-turbinate to tall-spined, occasionally patulous or globular ($H/B = (1.11)1.29\text{--}1.79$; $SH = (1.26)1.47\text{--}2.34$); spire outline straight; whorls rounded, suture impressed, periphery slightly angled; solid. Columella pillar straight or slightly concave; columella excavated; eroded parietal

area usually present. Sculpture of 8–12 approximately equidistant primary spiral grooves (incised lines) above periphery, continuing on base; grooves occasionally obsolete; rarely, ribs between grooves become raised and prominent at periphery; microstriae faint or absent; surface, especially spire, often eroded; growth lines weak. Protoconch rarely preserved, about 3 whorls, 375–425 μm length, sculptured by spiral rows of minute tubercles (Pilkington, 1971). Colour cream with pale to dark brown spiral lines (corresponding to spaces between grooves); rarely, lines are faint or narrow (Fig. 12F); occasionally entirely brown with pale grooves on base only; occasionally

cream with a broad peripheral brown band and few spiral brown lines on base (Fig. 12D); juveniles black or brown with one or more spiral white lines on base; aperture dark brown with basal white band.

Animal. Head, tentacles and sides of foot black. Opercular ratio 0.44–0.54. Penis (Fig. 13A–D): filament 0.5 total length of penis, smooth or slightly wrinkled, bluntly pointed, slightly swollen, reddish coloration at base of filament when live; sperm groove opens terminally; single mamilliform gland and adjacent large flap of penial glandular disc borne together on broad lateral branch of base; penial base often with black pigment. Euspermatozoa 79–86 μm ; paraspermatozoa (Fig. 13G,H) spherical, 10–13 μm diameter, containing large spherical granules and a curved, twisted or torus-shaped rod body. Pallial oviduct (Fig. 13E) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, within which portion adjacent to egg groove (translucent capsule gland) is differentiated as a ring; copulatory bursa large, opening near anterior end of straight section, extending back beneath capsule gland.

Spawn and development. Spawn (Fig. 13F) a transparent pelagic capsule 250 μm diameter, containing a single ovum 80 μm diameter, capsule with domed upper surface sculptured by 3 concentric rings, peripheral ridge and a basal circumferential flange; development planktotrophic; spawning season November to March (at Otago; Pilkington, 1971).

Radula (Fig. 4G,H). Relative radular length 3.5–5.6. Rachidian: length/width 1.18–1.30; major cusp elongate, rounded to slightly pointed at tip. Lateral and inner marginal: major cusps large, elongate, bluntly rounded to slightly pointed at tip. Outer marginal: 7–9 cusps.

Habitat. This species is most abundant in the southern areas of New Zealand, where it occupies a vertical range from the littoral fringe to the barnacle zone, and may even extend to the kelp (*Durvillea*) zone (at Otago; Batham, 1958; Morton & Miller, 1968). There is some downward migration during the spawning season (Pilkington, 1971). Although its upper vertical limit is below that of the frequently sympatric *A. antipodum*, it has a wider range of habitat; it reaches further down the shore, is common in sheltered and exposed sites, and extends further into turbid bays (Batham, 1956; Morton & Miller, 1968). Further north in South Island, its tidal range is more restricted than that of *A. antipodum* and its distribution is centred on more sheltered shores than that species, being most frequent on irregular rock with numerous crevices (at Banks Peninsula; Knox, 1953). In North Island, it is sparse on the east coast of Auckland, where it is restricted to open coasts, but more common on the Auckland west coast (Morton & Miller, 1968).

Range (Fig. 14). New Zealand, Auckland Islands, Chatham Islands. This species occurs throughout the two main islands of New Zealand (northernmost record: The Bluff, Ninety-Mile Beach, 34°41'S 172°54'E, AMS C406343), on Stewart Island (Port Pegasus, 47°09'S 167°42'E, MNZ M026145), Snares Islands (Rima Islet, 48°02'S 166°38'E, MNZ M058350), Auckland Islands (Rose Island, 50°31'S 166°15'E, MNZ M155923) and Chatham Islands (Waitangi Bay, 43°57'S 176°33'W, MNZ M110471; Powell, 1933b).

Remarks. The shell shows considerable variability in both shape and colour. Shape ranges from elongate to globular or even patulous. Possible correlation with environmental

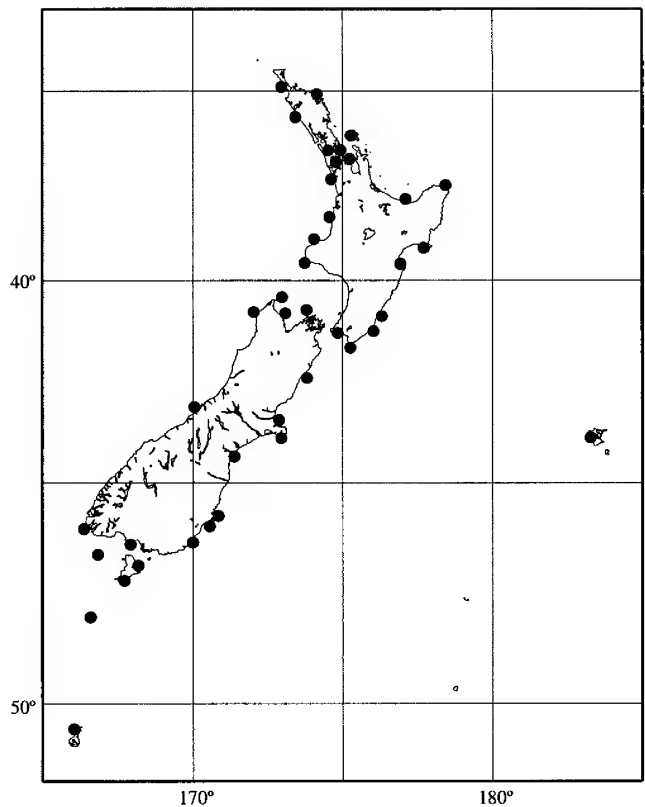


Fig. 14. Distribution of *Austrolittorina cincta*.

variables has not been recorded but, by analogy with other species (e.g., *A. unifasciata*) the wide-mouthed forms might be found on more exposed coasts.

Of the two species of *Austrolittorina* in New Zealand, *A. cincta* has the darker coloration and more southerly (i.e. higher latitude) distribution, whereas *A. antipodum* has a paler shell and more northerly distribution. This might be an example of climatic selection, with dark, heat-absorbing shells in cooler climates. A similar case has been noted in the intraspecific variation of *A. araucana* (Reid, 2002a) and another in the pair *Afrolittorina africana* and *A. knysnaensis* (described below).

This species is sympatric with *A. antipodum* throughout most of its range; however, its distribution is more southern, for it is more common in the south of its range (Suter, 1913) and extends to the Auckland Islands (where *A. antipodum* does not occur). In the north it does not reach the Three Kings Islands or the Kermadec Islands, in contrast to *A. antipodum*. The two species are readily discriminated by the brown colour or lined pattern of *A. cincta*; when, rarely, the pattern is faint or reduced to a peripheral band only, the base still retains a few brown lines close to the columella, and the spiral grooves are more pronounced than in *A. antipodum*. Anatomically, there is only a slight difference in the penial shape, the filament being slightly more pointed in *A. cincta*.

Austrolittorina araucana (d'Orbigny, 1840)

Littorina araucana d'Orbigny, 1840: 393–394; Atlas pl. 53, figs. 8–10 (Valparaíso, Chile, also entire coast as far as Arica, Pérou [Valparaíso, Chile, to Arica, Chile], restricted to Valparaíso (Reid, 2002a); lectotype (Reid, 2002a) BMNH 1854.12.4.365/1; 12 paralectotypes BMNH 1854.12.4.365/2, seen).

Nodilittorina araucana Reid, 2002a: 142–145, figs 16G, H (radula), 18A–J, 19A–C (penes), F (egg capsule), H (pallial oviduct), J, K (paraspermatozoa), 20 (distribution).
Austrolittorina araucana.—Williams *et al.*, 2003.

Taxonomic history. For full synonymy see Reid (2002a).

Diagnosis. Shell small, periphery rounded; sculpture of numerous fine spiral grooves, becoming obsolete; white to dark brown with pale basal band. Penial filament broad, with subterminal opening of sperm groove; mamilliform gland and small glandular disc on base. Pallial oviduct with simple loop of egg groove in albumen gland followed by flexure in capsule gland.

Range. Peru to southern Chile.

Remarks. This species is highly variable in shape, and ranges from white to blue-grey or uniform brown in colour, rarely with indistinct markings. Some pale shells are close in appearance to small examples of *A. unifasciata* and *A. fernandezensis*, but the three are allopatric and the pallial oviduct and penis of *A. araucana* are unique.

Molecular data have shown this species to be the basal member of the genus. Its separation from the four other living species was estimated at 40–73 million years ago, and therefore of sufficient age to be ascribed to the fragmentation of Gondwana (Williams *et al.*, 2003).

Afrolittorina Williams, Reid & Littlewood, 2003

Type species. *Littorina africana* Krauss, in Philippi, 1847.

Taxonomic history. Both *Afrolittorina africana* and *A. knysnaensis* were classified by Rosewater (1970) as members of his new subgenus *Littorina* (*Austrolittorina*), on the basis of their non-nodulose shells and *Nodilittorina*-like penes and radulae. The two remaining members, *A. praetermissa* and *A. acutispira* were transferred to *L. (Austrolittorina)* subsequently (Ponder & Rosewater, 1979). These four species were included in *Nodilittorina* (*Austrolittorina*) by Reid (2002a), as defined by the loop of the egg groove through the capsule gland of the pallial oviduct. A formal cladistic analysis of morphological characters of *Nodilittorina s.l.* (Reid, 2002b) did not support *Austrolittorina* as a monophyletic group. However, it did identify these four species as a clade, supported by the single unequivocal and unreversed synapomorphy of the loop of the egg groove through the jelly gland (elsewhere in the subfamily this feature is found only in *Melarhaphe neritoides*, in which the loop is elaborated into a spiral). DNA-sequence data have since shown unequivocally that the four species are not members of the *Austrolittorina* clade, but are the sister group of the northern-hemisphere genus *Littorina*, thus justifying the introduction of the new genus *Afrolittorina* (Williams *et al.*, 2003).

Diagnosis. Shell not nodulose; spiral striae or smooth; eroded parietal area usually absent; no pseudoumbilicus; pale with diffuse pattern of mottling, marbling or tessellation, rarely axially aligned. Cephalic tentacles with transverse lines, 1–2 longitudinal black stripes, or black. Penis with swollen filament; base bifurcate; single mamilliform gland; glandular disc of subepithelial glandular tissue may be large, minute or absent; if absent, epithelium

around mamilliform gland is tall and secretory; penial vas deferens an open groove. Rod bodies of paraspermatozoa long and straight, or small and irregular. In pallial oviduct egg groove makes a simple loop through albumen gland, large circular loop through capsule gland, smaller loop in jelly gland; copulatory bursa opens in posterior position. (After Williams *et al.*, 2003.)

Afrolittorina africana (Krauss, in Philippi, 1847)

Figs. 15–16, 17A,B, 18

Littorina africana Krauss, in Philippi, 1847: 199, *Littorina* pl. 4, fig. 10 (Caput Bona Spei [Cape of Good Hope, South Africa; restricted to Algoa Bay, Krauss, 1848]; lectotype (Janus, 1961) Stuttgart Museum ZI 0050275 (formerly MT 106; fig. 15A; seen) plus 1 paralectotype ZI 0050276; possible paralectotypes Senckenberg Museum SMF 314707/1 (Herbert & Warén, 1999); additional paralectotypes may be in Nationaal Natuurhistorisch Museum, Leiden [van Bruggen, 1992: 83]. Krauss, 1848: 102. Weinkauff, 1878: 37, pl. 4, figs. 5–6. Weinkauff, 1883: 218 (includes *A. knysnaensis*).

Littorina africana.—Reeve, 1857: *Littorina* sp. 37 (in part; pl. 8, fig. 37 is *L. unifasciata*). Nevill, 1885: 137. Bartsch, 1915: 120. Tomlin, 1923: 49. Dautzenberg, 1932: 60. Turton, 1932: 132, 133. Kilburn & Rippey, 1982: 50, pl. 10, fig. 1. Potter & Schleyer, 1991: pl. 2.2, 2.3 (radula).

Littorina (Melarhaphe) africana.—Adams & Adams, 1854: 314 (as *Melaraphe*). Tryon, 1887: 248–249, pl. 44, figs. 66–67 (as *Melaraphe*; in part; figs. 65, 68 are *Afrolittorina knysnaensis*; fig. 69 is *Echinolittorina quadricincta* Mühlfeld, 1824). Janus, 1961: 5 (as *Melaraphe*).

Littorina (Austrolittorina) africana.—Rosewater, 1970: 423, 476–477, pl. 364, figs. 11–16, pl. 365, fig. C (penis), pl. 368 (distribution). Kilburn, 1972: 399–401 (probably subspecies of *Austrolittorina unifasciata*).

Nodilittorina africana.—Bandel & Kadolsky, 1982: 3. Reid, 2002b: fig. 2a (penis).

Nodilittorina (?Echinolittorina) africana.—Reid, 1989: 99, fig. 10i (oviduct) (*A. knysnaensis* doubtfully included).

Nodilittorina (Austrolittorina) africana.—Reid, 2002a: 154.

Afrolittorina africana.—Williams *et al.*, 2003.

Littorina decollata Krauss, in Philippi, 1847: 196; *Littorina* pl. 4, fig. 3 (Ora Natal Africae [coast of Natal, South Africa]; lectotype (Janus, 1961) Stuttgart Museum ZI 0050277 (formerly MT 107; fig. 15F; seen) plus 26 paralectotypes ZI 0050278; possible paralectotypes Senckenberg Museum SMF 314709/3 and uncatalogued (Herbert & Warén, 1999); 15 possible paralectotypes MCZ 154113; 2 paralectotypes ZMA; additional paralectotypes may be in Nationaal Natuurhistorisch Museum, Leiden [van Bruggen, 1992: 83]. Krauss, 1848: 102. Küster, 1856: 9, pl. 1, figs. 14–15. Weinkauff, 1878: 28. Weinkauff, 1883: 219 (in part; includes *A. knysnaensis*).

Littorina (Melarhaphe) decollata.—Adams & Adams, 1854: 314 (as *Melaraphe*). Janus, 1961: 5–6 (as *Melaraphe*).

Littorina decollata.—Reeve, 1858: *Littorina* sp. 92, pl. 17, fig. 92. Sowerby, 1892: 36. Turton, 1932: 132.

Littorina caerulea.—Tenison Woods, 1879: 65–72 (as *coerulea*; not *Turbo caerulea* Lamarck, 1822 = *Melarhaphe neritoides*; in part; includes *Austrolittorina unifasciata*, *Austrolittorina antipodum*, *Afrolittorina praetermissa*, *Littoraria mauritiana*, *L. undulata*, *M. neritoides*).

Littorina knysnaensis.—Sowerby, 1892: 36 (not *Littorina knysnaensis* Krauss, in Philippi, 1847 = *A. knysnaensis*; in part; includes *A. knysnaensis*).

?*Littorina perplexa* Turton, 1932: 133, pl. 28, fig. 960 (Port Alfred, South Africa; holotype OUM, seen).

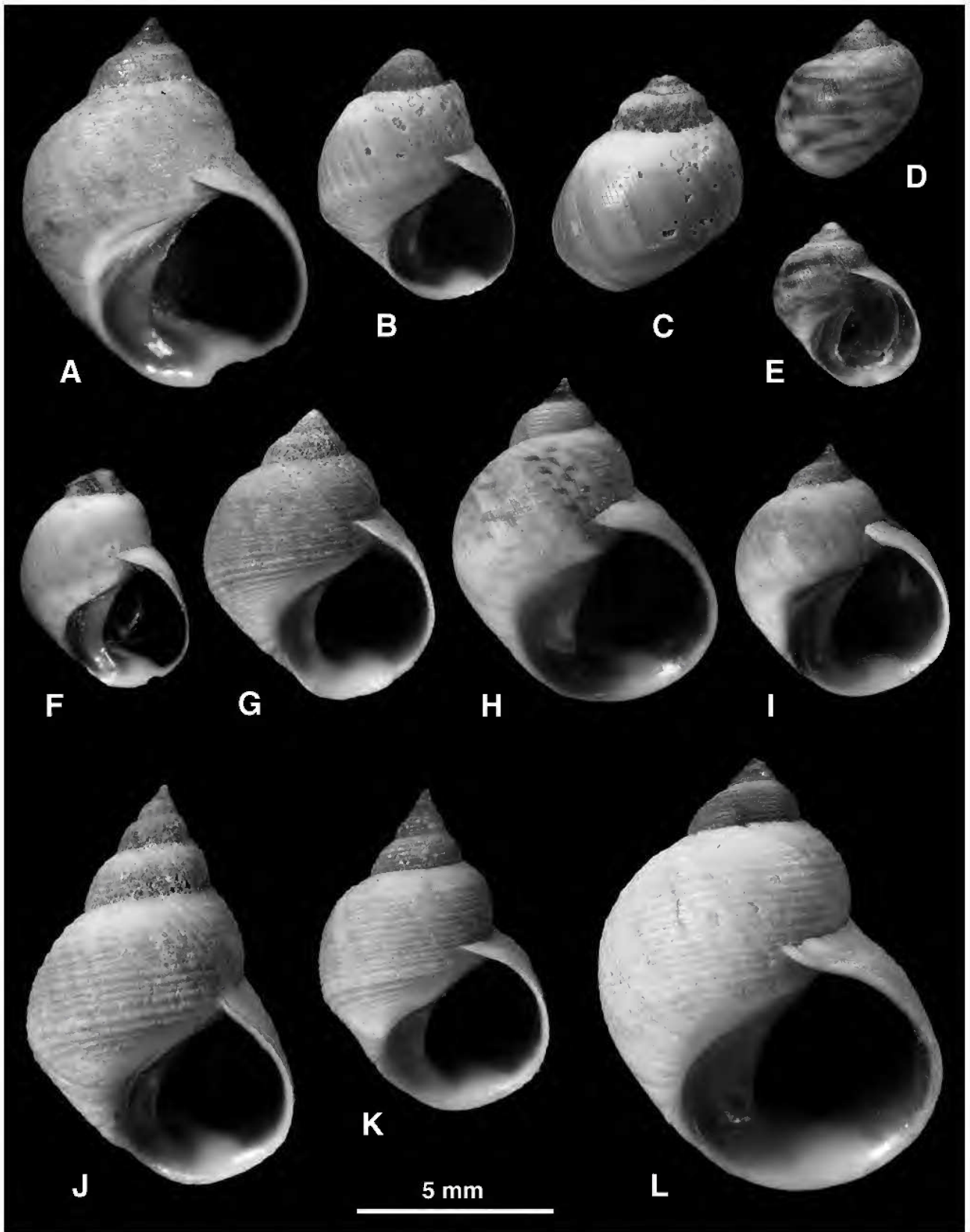


Fig. 15. *Afrolittorina africana*: (A) Lectotype of *Littorina africana* Krauss, in Philippi, 1847; no locality (Stuttgart Museum ZI 0050275). (B) Port Elizabeth, South Africa (BMNH 20030415). (C) Flat rock surfaces and pools, Umngazana, South Africa (BMNH 20030416). (D,E) Umhlanga Rocks, South Africa (BMNH 20030417). (F) Lectotype of *Littorina decollata* Krauss, in Philippi, 1847; no locality (Stuttgart Museum ZI 0050277). (G,K) Concrete wall, Umngazana, South Africa (BMNH 20030418). (H,I,L) Richards Bay, South Africa (BMNH 20030419). (J) Arniston, South Africa (BMNH 20030420).

Taxonomic history. Krauss (1848) described three new littorinids from South Africa, *Litorina africana*, *L. decollata* and *L. knysnaensis* but, owing to his habit of sending specimens and manuscript names to colleagues, the names and descriptions had appeared a year earlier in the monograph of *Litorina* by Philippi (1847). Krauss was credited with authorship in this earlier publication (see biographical notes on Krauss and discussion of his taxa by Herbert & Warén, 1999). Later authors maintained these taxa as distinct until the first revision by Tryon (1887), who correctly synonymized *L. decollata* with *L. africana* (thereby establishing the valid name for this species, despite the page priority of *L. decollata*). Among later authors, only Sowerby (1892), Turton (1932) and Janus (1961) have continued to regard *L. decollata* as a distinct species.

The shells of the two species are usually easily separable, so it is surprising that there has been a long history of confusion and combination of *A. africana* and *A. knysnaensis*. Weinkauff (1883) and Tryon (1887) both regarded *knysnaensis* as a variety of *L. africana*, whereas Sowerby (1892) combined both under the former name. Bartsch (1915) recognized both species, yet described elongate examples of *A. knysnaensis* as *L. africana tryphena*. Although Rosewater (1970) clearly described the characteristic shells of the two species, Hughes (1979) once again combined the two as varieties of *L. africana*. The evidence for this was that “the complete range of intermediate forms in shell colour and morphology, and the absence of differences in radulae, penial morphology or habitat suggest that these forms represent a dimorphic species showing a genetic cline correlated with latitude” (Hughes, 1979). The relative proportions of the blue-grey *A. africana* and brown *A. knysnaensis* do indeed change from 0 to 100% along the South African coast between False Bay and Natal. However, although the shell of *A. knysnaensis* can sometimes be pale in colour, the two species remain distinct in shell shape and sculpture. Most significantly, the penes are distinct, particularly in their pigmentation, as observed by Hughes himself. Subsequent authors (Kilburn, 1972; Bandel & Kadolsky, 1982) retained the two as distinct species, although Reid (1989) doubtfully synonymized them.

The identity of *Littorina perplexa*, described by Turton (1932) from Port Alfred, is puzzling. Rosewater (1970) listed it in the synonymy of “*Littorina punctata* (Gmelin, 1791)” (presently interpreted as a complex of three species, including *Echinolittorina punctata*; Reid, 2002b). Noting that *E. punctata* s.l. does not occur in South Africa, Kilburn (1972) interpreted *L. perplexa* as a form of *A. africana* with a patterned shell. The unique holotype is a beachworn shell 1.9 mm in height, of about two teleoconch whorls, with a low-turbinate shape, weak spiral grooves, eroded apex and well-developed tessellated pattern. At this small size none of the three turbinate littorinids recorded from Port Alfred (*A. africana*, *A. knysnaensis*, *Littoraria intermedia* [Philippi, 1846]) has been seen to develop a distinct tessellated pattern of this kind, so although Kilburn’s attribution is possible, it can be doubted. The shell does indeed resemble a juvenile specimen of the *E. punctata* complex, perhaps accidentally transported to Port Alfred.

Reeve (1857) inadvertently described and figured a shell of *Austrolittorina unifasciata* as *Littorina africana*, as noted by Smith (1884, as *L. mauritiana*). The South African species has occasionally been united with species of

Austrolittorina as a single taxon (Tenison Woods, 1879; see Taxonomic History of *Austrolittorina unifasciata*). Kilburn (1972) revived this idea, suggesting that *Littorina africana* might prove to be a subspecies of *Littorina unifasciata*, a circumpolar taxon.

Diagnosis. Shell small, turbinata, usually sculptured with fine spiral threads; white with broad blue-grey band above periphery, sometimes with additional fine, pale brown tessellation. Penis with bluntly blade-shaped, red-brown (greyish black when preserved) filament; mamilliform gland on base, but no glandular disc. Pallial oviduct with three consecutive loops of egg groove, in albumen gland, capsule gland and in terminal portion of oviduct.

Material examined. 52 lots (6 AMS, 3 USNM, 38 BMNH, 1 IRSNB, 1 ZMA, 1 MNHNP, 2 NM), including 16 penes, 3 sperm samples, 16 pallial oviducts, 6 radulae.

Shell (Fig. 15). Mature shell height 3.7–12.0 mm (13.5 mm, Rosewater, 1970). Shape globular to turbinata (H/B = 1.20–1.66; SH = 1.18–1.91); spire outline slightly concave at apex; whorls well rounded, suture distinct, periphery rounded or slightly angled; moderately solid. Columella pillar straight to slightly concave; columella broad, slightly excavated; eroded parietal area usually absent but may be present in low-spined shells. Sculpture of numerous fine spiral threads and striae (not clearly differentiated into primary grooves, ribs and microstriae); on early teleoconch whorls 8–11 threads visible above suture, with striae between; on last whorl numerous closely spaced coarse striae over entire whorl, of which 15–27 may be raised as narrow cords; periphery not marked by an enlarged rib; sometimes almost smooth with only faint spiral striae; growth lines may be present towards end of last whorl; spire often eroded. Protoconch rarely preserved, about 0.34 mm diameter, 3 whorls. Colour white to cream, with broad spiral band of blue-grey from just below suture to below periphery; darker pattern may be absent, but fine tessellation of yellow or pale brown is often faintly visible over entire surface of last whorl (Fig. 15G,H); rarely, pattern is developed into conspicuous oblique, spiral or zigzag brown lines (Fig. 15D,E); eroded spire blackish brown; aperture dark brown with basal white band; first 2 whorls of teleoconch fawn.

Animal. Head and sides of foot grey to black; tentacles with fine black transverse lines (sometimes faint or absent). Opercular ratio 0.37–0.44. Penis (Fig. 16A–J): filament 0.5–0.6 total length of penis, bluntly blade-shaped and slightly swollen, coloured red brown in life (dark greyish black in preserved specimens) by subepithelial glandular tissue; sperm groove open almost to filament tip; single mamilliform gland borne on lateral branch of base; glandular disc absent; instead the epithelium around the papilla of the mamilliform gland is tall and glandular; base unpigmented. Euspermatozoa length unknown; paraspermatozoa (Fig. 16M) spherical to oval, 11–19 µm diameter, containing large spherical granules and single hexagonal or irregular rod-body, rarely projecting from cell. Pallial oviduct (Fig. 16K,L) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, of which a small distal part may be differentiated as reddish translucent capsule gland; additional simple loop of glandular material between capsule gland and terminal portion of pallial

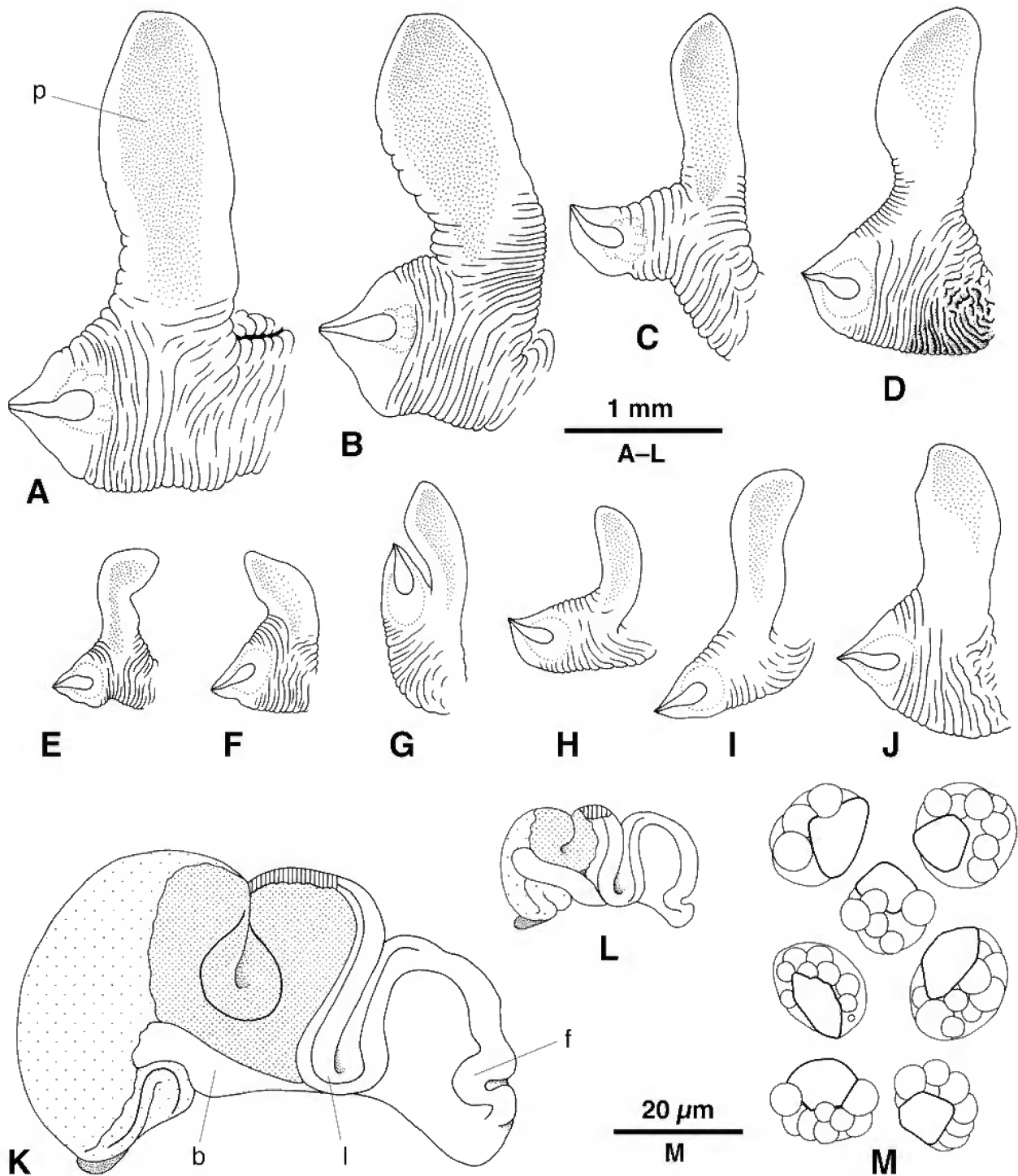


Fig. 16. *Afrolittorina africana*: (A–J) Penes. (K, L) Pallial oviducts. (M) Paraspermatozoa from one specimen. (A–C, M) Munster, South Africa (BMNH 20030412). (E, F, L) Umngazana, South Africa (from “*decollata*” shell form; BMNH 20030422). (G–J) Umhlanga Rocks, South Africa; ([G, H] from crevice-dwelling shell form, BMNH 20030423; [I] from normal shell form; BMNH 20030424). (J) Richards Bay, South Africa (BMNH 20030425). (K) Salt Rock, South Africa (BMNH 20030426). Shell heights: (A) 10.4 mm, (B) 10.5 mm, (C) 5.8 mm, (D) 6.7 mm, (E) 4.7 mm, (F) 5.4 mm, (G) 4.2 mm, (H) 3.7 mm, (I) 5.0 mm, (J) 8.2 mm, (K) 10.2 mm, (L) 5.2 mm. Abbreviations: (b) copulatory bursa; (f) terminal flexure of egg groove; (l) loop of egg groove between capsule gland and straight section of pallial oviduct; (p) dark pigment of subepithelial glandular tissue visible by transparency in penial filament. Shading conventions as in Fig. 3.

oviduct; small flexure of egg groove just before opening to mantle cavity; large copulatory bursa separates in a posterior position and continues back to overly capsule gland.

Spawn and development. Not recorded; pelagic spawn and

planktotrophic development predicted from dimensions of protoconch and large capsule gland (Reid, 1989).

Radula (Fig. 17A, B). Relative radular length 4.1–7.6 (4.03, s.e. 0.33; Potter & Schleyer, 1991). Rachidian: length/width

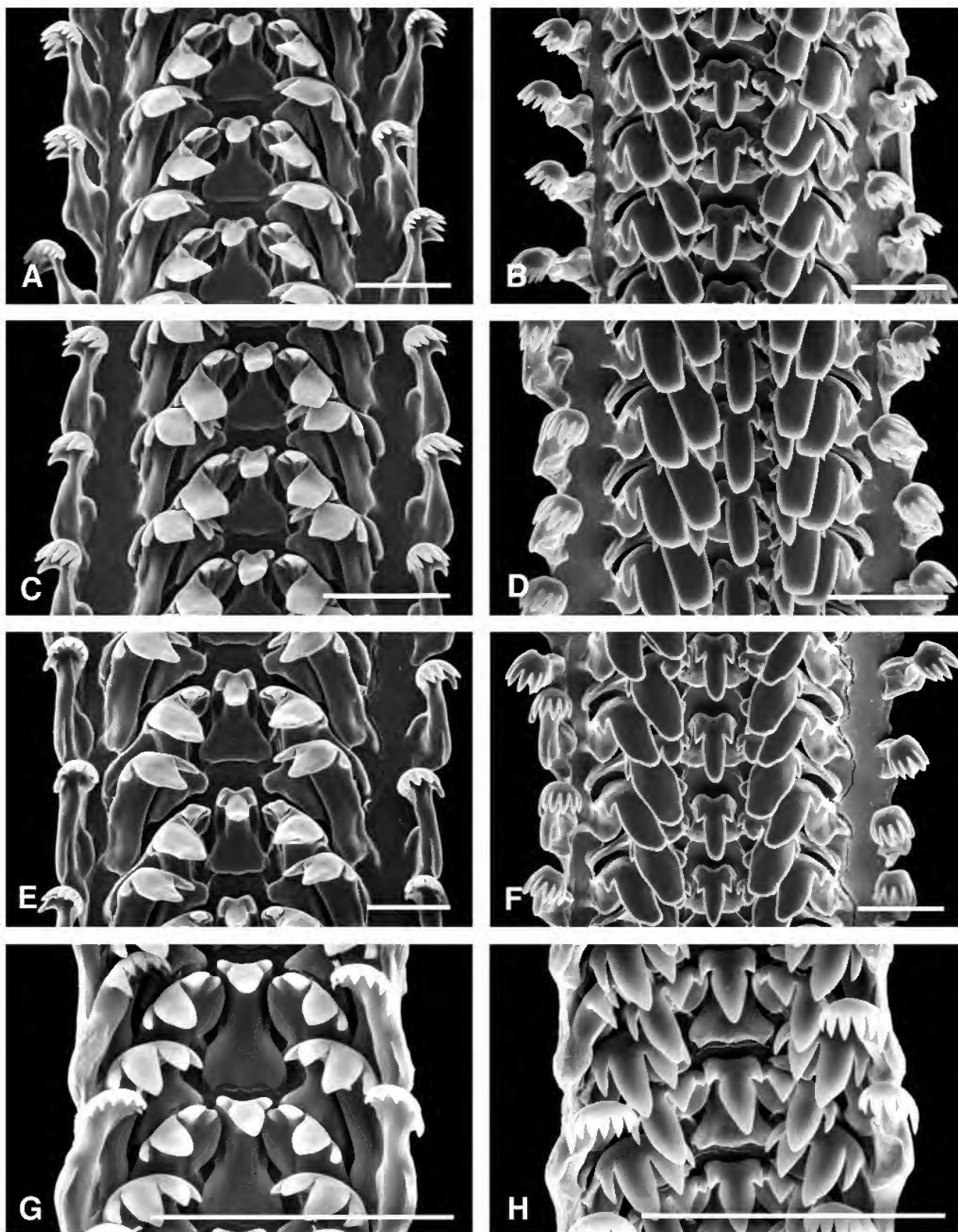


Fig. 17. Radulae; views of same specimen flat (A,C,E,G) and at 45° from anterior end (B,D,F,H). (A,B) *Afrolittorina africana*, Salt Rock, South Africa (BMNH 20030426; shell H = 10.2 mm). (C,D) *Afrolittorina knysnaensis*, Cape Agulhas, South Africa (BMNH 20030427; shell H = 9.3 mm). (E,F) *Afrolittorina praetermissa*, Port Campbell, Victoria, Australia (AMS C388111; shell H = 8.5 mm). (G,H) *Afrolittorina acutispira*, North Harbour, Sydney, NSW, Australia (BMNH 20030446; shell H = 3.9 mm). Scale bars = 50 µm.

1.19–1.48; major cusp elongate, rounded to pointed at tip. Lateral and inner marginal: major cusps large, elongate, bluntly rounded to truncate at tip. Outer marginal: 8–10 cusps (10–11; Potter & Schleyer, 1991).

Habitat. *Afrolittorina africana* dominates the upper shore on open coasts in the Transkei and Natal, reaching densities of up to 6000 m⁻² in the upper barnacle zone (Dye, 1988). The vertical tidal range is wide, from mean low water of neap tide to the littoral fringe; recruitment occurs on the horizontal platforms of the lower shore and is followed by upward migration (Eyre & Stephenson, 1938; Potter, 1987; Potter & Schleyer, 1991). In Natal, the northern part of the range, the vertical distribution is shifted lower on the shore, perhaps as an effect of higher temperatures (Kilburn & Rippey, 1982; McQuaid & Sherman, 1988; McQuaid, 1992). At East London, where both *A. africana* and *A. knysnaensis* are common, the former dominates in the lower parts of the littorinid zone and extends slightly lower on the shore (Eyre *et al.*, 1938). Although most abundant a range of rocky substrates on open coasts, the species can also be found in sheltered estuaries and on wooden posts (Kilburn, 1972). Juveniles feed on bacteria and diatoms, and adults mainly on lichens and blue-green algae (Potter & Schleyer, 1991).

Range (Fig. 18). southwestern Indian Ocean from near Cape Town to Natal, southern Mozambique and southeastern Madagascar. The range limits in South Africa are St James, False Bay (34°07'S 18°27'E, BMNH 20030448; Eyre, 1939) and Cape Vidal, Natal (28°08'S 32°33'E, BMNH 20030449), but the species is relatively uncommon (in comparison with the sympatric *A. knysnaensis*) further south and east than Port St Johns (31°38'S 29°33'E; Hughes, 1979), and becomes rare at Cape Agulhas (Stephenson, 1944). To the

north of Cape Vidal there is a long stretch of unsuitable sandy coastline, but there are three records from southern Mozambique: Inhaca Island (26°02'S 32°58'E, USNM 637363); Tofo (23°51'S 35°33'E, AMS); Morrungulo, near Massinga (23°15'S 35°22'E, NM G4627). The species just reaches southeastern Madagascar, where it is recorded from Ambovombe, (25°11'S 46°05'E, IRSNB) and Flacourt, Fort Dauphin (25°02'S 47°00'E, USNM 678834).

Remarks. This species is variable in shell characters and at least three intergrading forms can be recognized (see Kilburn, 1972, for discussion). The typical form is the largest, a turbate shell with sculpture varying from incised lines to raised threads (Fig. 16A,G–L). The colour is white with a broad blue-grey band from below the suture to below the periphery. In the northern part of the range (at Port St Johns, in Natal and Mozambique) this may be overlain by a faint, fine, tessellated pattern of yellow or pale brown (Fig. 16G–I,K). The form described by Krauss as *Litorina decollata* is a small, low-spined shell with smooth surface, white with a broad blue-grey band, but no patterning (Fig. 16B,C,F). Kilburn (1972) noted that the *decollata* form occurred both sporadically among populations of the typical form and in pure populations, and that its occurrence was not correlated with degree of wave exposure. In BMNH two collections from the same locality, Umngazana, suggest a different correlation. A sample from concrete walls (BMNH 20030418) at this open-coast locality is of the typical form, whereas a sample from flat surfaces and pools (BMNH 20030416) is of the *decollata* form. In members of the *Echinolittorina aspera* species group from the eastern Pacific, individuals in pools at the top of the eulittoral zone are stunted and more smooth than those on rocks in the littoral fringe (Reid, 2002a). Stunted individuals in pools have also been noted in *Littoraria pintado pullata*

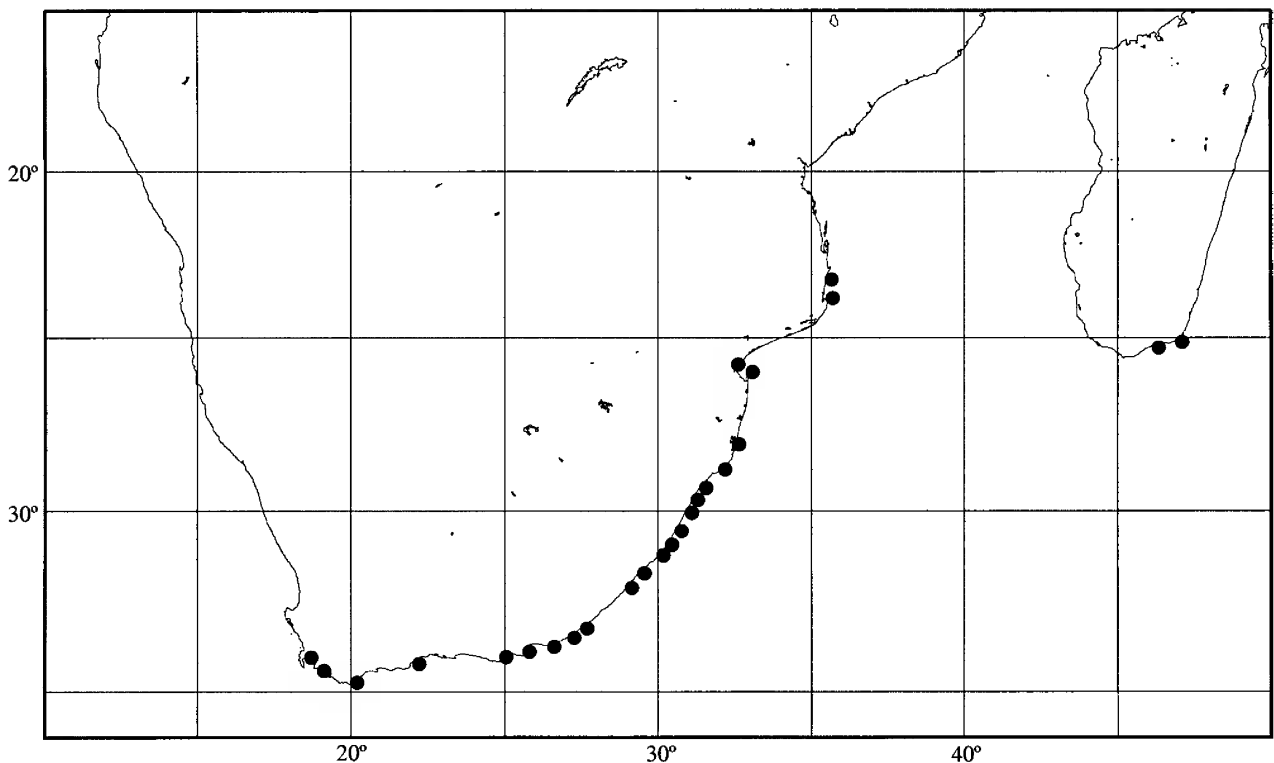


Fig. 18. Distribution of *Afrolittorina africana*.

(Carpenter, 1864) (Reid, 1999). In both these cases, as in *A. africana*, the species has planktotrophic development, so that genotypic differentiation between the shell forms is unlikely and an ecophenotypic effect may explain this pattern of small-scale variation.

Another distinctive form with a strong pattern of brown spiral lines, zigzags and coarse tessellation was mentioned by both Kilburn (1972) and Hughes (1979). Specimens collected by Hughes at Umhlanga Rocks, Natal, are small (less than 5 mm), smooth, low-spined and of patulous shape (Fig. 16D,E; BMNH 20030423). These were found in crevices and contrasted with the common typical form at the same locality (BMNH 20030424). The dimorphism of the shells at this locality is so striking that a pair of sympatric species might be suspected, yet no anatomical differences could be detected in the present study (Fig. 16G–I). Hughes (1979) pointed out the parallel with the “*neglecta*” ecotype of *Littorina saxatilis* (Olivi, 1792) (equivalent to the “barnacle ecotype” of Reid, 1996). The interpretation of these specimens as an ecophenotype of *A. africana* is supported by the finding of identical sequences of the 12S mitochondrial gene in both (S.T. Williams, unpublished).

Distinction from the partially sympatric *A. knysnaensis* is described in the Remarks on that species.

Phylogenetic analysis of morphological characters identified *A. africana* and *A. knysnaensis* as sister species on the basis of the tall, secretory epithelium surrounding the mamilliform penial gland (which may serve the function of the absent subepithelial glandular disc), and this is a unique synapomorphy (Reid, 2002b). This relationship was supported by DNA-sequence analysis that estimated that the two species may have diverged more than 10 million years ago (Williams *et al.*, 2003). These two are in turn the sister group of the pair of Australian members of *Afrolittorina*, and the divergence time between the African and Australian pairs was estimated as 29–55 million years.

Afrolittorina knysnaensis (Krauss, in Philippi, 1847)

Figs. 17C,D, 19–21

- Littorina knysnaensis* Krauss, in Philippi, 1847: 196, *Littorina* pl. 4, fig. 4 (Caput Bona Spei ad regionem fluminis Knysna [Cape of Good Hope near Knysna River, South Africa]; lectotype (Janus, 1961) Stuttgart Museum ZI 0050273 (formerly MT 108; fig. 19A; seen) plus 30 paralectotypes ZI 0050274; 20 paralectotypes MCZ 154114; possible paralectotypes Senckenberg Museum uncatalogued (Knysna Fluss) and SMF 314706/7 (Algoa Bay) (Herbert & Warén, 1999); additional paralectotypes may be in Nationaal Natuurhistorisch Museum, Leiden (van Bruggen, 1992). Krauss, 1848: 102. Weinkauff, 1882: 71–72, pl. 9, figs. 10–11.
- Littorina (Melarhaphé) knysnaensis*.—Adams & Adams, 1854: 314 (as *Melarhaphé*). Janus, 1961: 6 (as *Melarhaphé*).
- Littorina knysnaensis*.—Reeve, 1857: *Littorina* sp. 75, pl. 14, fig. 75a,b. Troschel, 1858: 134 (radula) (as *knysnaniensis*). Sowerby, 1892: 36 (in part; includes *A. africana*). Bartsch, 1915: 120. Turton, 1932: 132, pl. 28, fig. 955. Kilburn & Rippey, 1982: 50, pl. 10, fig. 2. Potter & Schleyer, 1991: pl. 2.1 (radula).
- Littorina (Melarhaphé) africana* var. *knysnaensis*.—Tryon, 1887: 249, pl. 44, figs. 65, 68 (as *Melarhaphé*).
- Littorina (Austrolittorina) knysnaensis*.—Rosewater, 1970: 423, 478–479, pl. 364, figs. 17–23, pl. 365, fig. D (penis), pl. 369 (distribution). Kilburn, 1972: 402.
- Nodilittorina (Nodilittorina) knysnaensis*.—Bandel & Kadolsky, 1982: 37–38.
- Nodilittorina (Austrolittorina) knysnaensis*.—Reid, 2002a: 154.

Afrolittorina knysnaensis.—Williams *et al.*, 2003.

Littorina picea Reeve, 1857: *Littorina* sp. 83, pl. 15, fig. 83 (no locality; type locality designated as South Africa (Rosewater, 1970); holotype BMNH 1968320, seen).

Littorina africana.—Weinkauff, 1883: 218 (not Krauss, in Philippi, 1847; in part; includes *A. africana*).

Littorina decollata.—Weinkauff, 1883: 219 (not Krauss, in Philippi, 1847 = *A. africana*; in part; includes *A. africana*).

Littorina africana tryphena Bartsch, 1915: 120, pl. 38, fig. 6 (Port Alfred, South Africa; holotype USNM 187091, seen; paratype USNM 664353, not seen [Rosewater, 1970]).

Littorina tryphena.—Turton, 1932: 132.

Littorina rietensis Turton, 1932: 131, pl. 28, fig. 948 (Port Alfred, South Africa; holotype OUM, seen).

Littorina mauritiana acuta.—Turton, 1932: 131, pl. 28, fig. 950 (not *Littorina acuta* Menke, 1843 = *A. unifasciata*).

Littorina kowiensis Turton, 1932: 132, pl. 28, figs. 956 (Port Alfred, South Africa; 5 syntypes OUM, seen).

Littorina africana pica “Reeve” Turton, 1932: 133 (unjustified emendation of *L. picea* Reeve, 1857).

Littorina indistincta Turton, 1932: 133, pl. 28, fig. 959 (Port Alfred, South Africa; 2 syntypes OUM, seen).

Littorina punctata.—Penrith & Kensley, 1970a: 191–239 (not *Turbo punctatus* Gmelin, 1791 = *Echinolittorina punctata*). Penrith & Kensley, 1970b: 243–268 (in part, includes *E. punctata*, see Kilburn, 1972; personal observation of voucher material in SAM).

Taxonomic history. Although recognized as a distinct species by most authors throughout its history, there has been a recurring tendency to synonymize it with the sympatric *A. africana* (Weinkauff, 1883; Tryon, 1887; Sowerby, 1892; Hughes, 1979; see Taxonomic History of *A. africana*).

Reeve (1857) named a small, unlocalized shell of this species as *Littorina picea*; this was erroneously synonymized with *Littorina decollata* (= *A. africana*) by Weinkauff (1883), but correctly identified as *L. knysnaensis* by Tryon (1887). There has been confusion about the identification of the holotype of this taxon. Reeve (1857) referred to a single shell, but Rosewater (1970) incorrectly selected a “lectotype” from among “3 syntypes”. An original label records that the two additional shells were added in 1877 (BMNH 1877.4.30.1, obtained from Sowerby). Rosewater (1970: 479, pl. 364, figs. 19–20) selected and figured the best specimen as “lectotype”, but this is not in fact Reeve’s holotype. One of the remaining two shells is a small, eroded, specimen of *A. knysnaensis* that is blackish brown above the periphery, paler near the suture and shows traces of the characteristic speckled pattern only on the base. This shell exactly matches Reeve’s original figure in its pattern of erosion and growth lines, and corresponds with his description of a plain black shell with a slightly rugose surface; it is clearly the holotype.

Various unusual forms of this species have been named. *Littorina africana tryphena* Bartsch, 1915 was based on two beach-worn shells of unusually high-spined, pupoidal shape; similar specimens have been found to contain trematode parasites (see Remarks below). Turton (1932) named several small or beach-worn shells: *Littorina rietensis* is a rare form with carinate ribs; *L. kowiensis* is brown without the normal speckled pattern; *L. indistincta* was based on small brown juveniles about 2 mm tall that are probably of this species.

Bandel & Kadolsky (1982) doubtfully listed *Turbo dispar* Montagu, 1815, described from Poole, England, in the synonymy of *A. knysnaensis*, but recommended that it

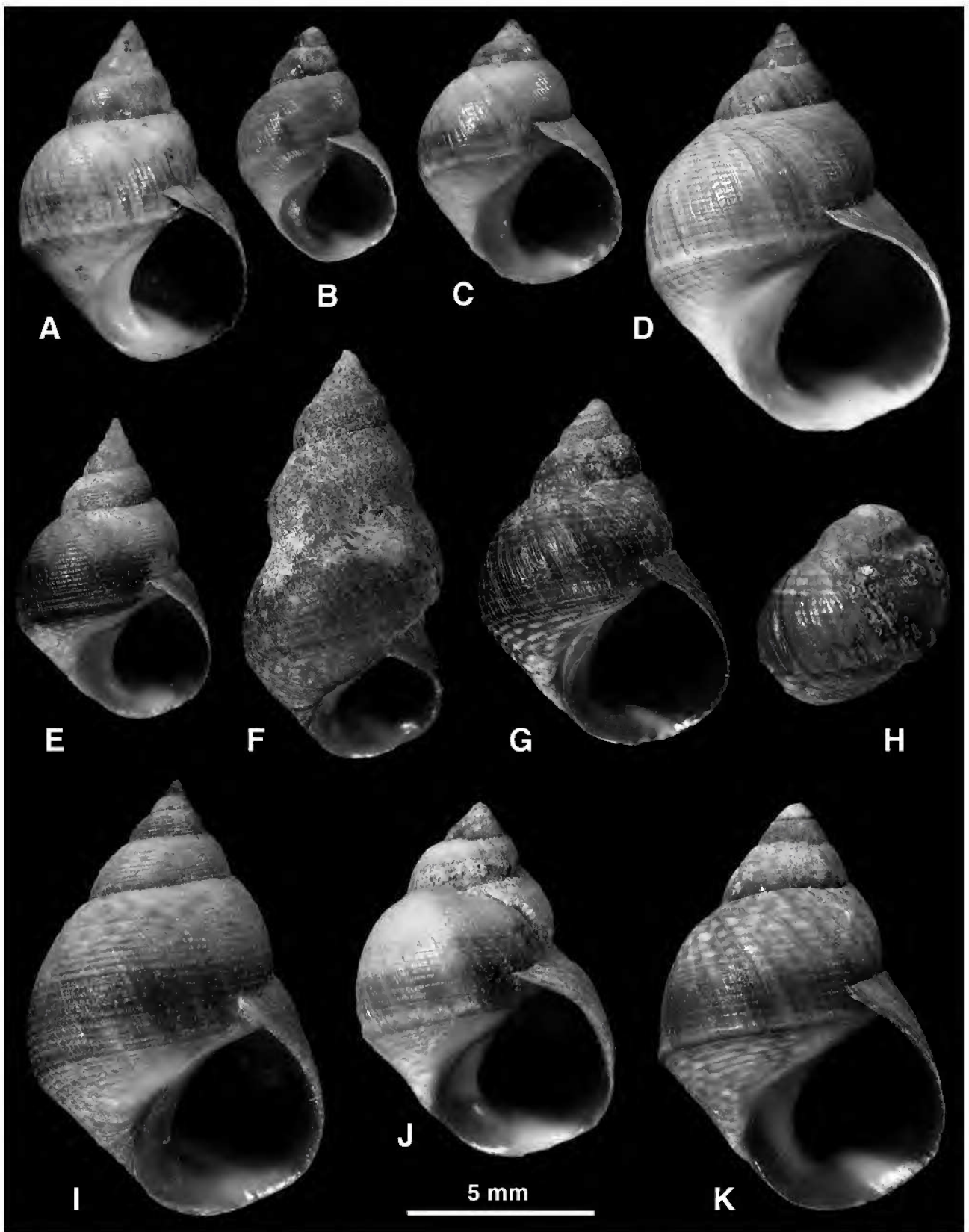


Fig. 19. *Afrolittorina knysnaensis*: (A) lectotype of *Litorina knysnaensis* Krauss, in Philippi, 1847; no locality (Stuttgart Museum ZI 0050273). (B,C) Brent, South Africa (BMNH 20030428). (D) Hermanus, South Africa (BMNH 20030429). (E) Umngazana, South Africa (BMNH 20030430). (F,I–K) Arniston, South Africa (BMNH 20030431). (G) Walvis Bay, Namibia (BMNH 20030433). (H) Lüderitz, Namibia (SAM A31286).

should be considered a forgotten name. Nevertheless, this can be recognized as *Melarhaphe neritoides* from the original figure and description (“obsoletely striated in a spiral direction” Montagu, 1815; not “spiral furrows”, Bandel & Kadolsky, 1982), as confirmed by a specimen from Montagu’s collection in the Royal Albert Memorial Museum, Exeter, England (no. 4202).

Schniebs (2000) identified the holotype of *Phasianella tessellata* Anton, 1838 as *Littorina knysnaensis*, but examination has shown this to be *Echinolittorina punctata* s.st.

Diagnosis. Shell moderately large, high-turbinate, angled at periphery, usually sculptured with fine spiral striae; pale, with fine red-brown speckling and broad bark brown band above periphery. Penis with rounded, slightly swollen filament, slight grey subepithelial glandular tissue distally, crimped lips of sperm groove; mamilliform gland on base, but no glandular disc. Pallial oviduct with three consecutive loops of egg groove, in albumen gland, capsule gland and in terminal portion of oviduct.

Material examined. 71 lots (7 AMS, 41 BMNH, 1 IRSNB, 8 ZMA, 1 MNHNP, 7 NM, 6 SAM), including 22 penes, 3 sperm samples, 11 pallial oviducts, 5 radulae.

Shell (Fig. 19). Mature shell height 3.8–19.2 mm. Shape high-turbinate (H/B = 1.26–1.61; SH = 1.29–1.92; exceptionally tall-spined specimens contain trematode parasites, H/B = 1.98, SH = 2.36; some eroded shells can appear almost globular, H/B = 1.10, SH = 1.41); spire outline slightly concave at apex; whorls moderately rounded, suture distinct, periphery angled, sharply so in juveniles, but sometimes rounded; moderately solid. Columella pillar slightly concave; columella broad, slightly excavated; eroded parietal area absent. Sculpture of numerous fine spiral elements (usually not clearly differentiated into primary grooves, ribs and microstriae); on penultimate whorl 10–13 threads visible above suture; on last whorl numerous closely spaced flat striae over entire whorl, of which 20–27 may be raised as threads; periphery marked by an enlarged riblet; occasionally almost smooth with only faint impressed spiral lines and microstriae; growth lines weak; spire often eroded. Protoconch rarely preserved, 0.34–0.43 mm diameter, 3 whorls. Colour variable, from pale grey to almost black; most commonly grey to cream ground colour, with fine red-brown speckling, palest on base, but darkening to form a broad, almost solid, brown to black band at and above periphery; palest shells grey to white, with only faint brown speckling or fine spiral lines, rarely unpatterned; darkest shells black with white speckling on base; aperture dark brown with basal white band; first 2 whorls of teleoconch brown.

Animal. Head and sides of foot grey to black; tentacles with fine black transverse lines (sometimes faint or absent). Opercular ratio 0.51–0.62. Penis (Fig. 20A–G): filament about 0.5 total length of penis, wrinkled and therefore not clearly differentiated from base, rounded and slightly expanded distally, slightly swollen, small patch of grey subepithelial glandular tissue may be visible distally; sperm groove open to filament tip, lips of groove crimped near tip; single mamilliform gland (rarely 2) borne on lateral branch of base; glandular disc absent; instead the epithelium around the papilla of the mamilliform gland is tall and

glandular; base may be slightly pigmented. Euspermatozoa length unknown; paraspermatozoa (Fig. 20I) oval, 14–21 µm long, containing large spherical granules and single elongate, straight, blunt-ended rod-body 24–48 µm long projecting from cell. Pallial oviduct (Fig. 20H; not as illustrated by Gosliner, 1981) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, of which a small distal part may be differentiated as reddish translucent capsule gland; additional simple loop of glandular material between capsule gland and terminal portion of pallial oviduct; small flexure of egg groove just before opening to mantle cavity; large copulatory bursa separates in a posterior position and continues back to overlying capsule gland.

Spawn and development. Not recorded; pelagic spawn and planktotrophic development predicted from egg size (87 µm, McQuaid, 1981a), from dimensions of protoconch and large capsule gland (Reid, 1989) and from low genetic differentiation on a geographical scale (Grant & Lang, 1991); continuous recruitment recorded at False Bay (McQuaid, 1981a).

Radula (Fig. 17C,D). Relative radular length 3.2–5.7 (5.59, s.e. 0.27; Potter & Schleyer, 1991). Rachidian: length/width 1.00–1.27; major cusp elongate to rectangular, bluntly rounded at tip. Lateral and inner marginal: major cusps large, elongate to rectangular, truncate at tip. Outer marginal: 7–9 cusps.

Habitat. On the rocky coasts of Namibia and South Africa (south of the Transkei) this is a dominant species on the upper shore. It is abundant across a wide zone from the littoral fringe down to the barnacle belt, extending to mean low water of neap tides (Stephenson *et al.*, 1937; Bokenham *et al.*, 1938; Bright, 1938; Stephenson *et al.*, 1940; Penrith & Kensley, 1970a,b, as *Littorina punctata*; Kensley & Penrith, 1980; McQuaid, 1981a, 1992). The vertical range is less wide on shores of moderate exposure, and the species is absent from sheltered and muddy bays (Penrith & Kensley, 1970a, as *Littorina punctata*). Settlement occurs mainly at the top of the shore, to avoid heavy wave action, although some settlement also takes place in crevices at lower levels; adults move downwards as they grow, to reach more abundant food (McQuaid, 1981b). Where both species occur, *A. knysnaensis* and *A. africana* show broad overlap of their vertical ranges (Hughes, 1979), although at East London the former has a higher vertical limit (Eyre *et al.*, 1938). The temperature relations of these two species differ, *A. knysnaensis* attaining higher tissue temperatures when attached by mucus in full sun, as a consequence of its darker coloration; it therefore occurs mainly in shaded microhabitats (McQuaid & Scherman, 1988).

Range (Fig. 21). Namibia and South Africa. On the Atlantic coast the northernmost samples examined are from Honolulu (20°36'S SAM A31185) and Rocky Point (18°59'S SAM A31184) (as also recorded by Kilburn, 1972). On the Natal coast the northernmost records are one specimen from Umhlali (29°20'S 31°14'E, Stephenson, 1947), one shell from Amanzimtoti (30°03'S 30°53'E, BMNH) and another from Umkomaas (30°12'S 30°48'E, NM 8604; also Kilburn, 1972), but the species is relatively uncommon (in comparison with the sympatric *A. africana*) to the north of Port St Johns (31°38'S 29°33'E; Hughes, 1979, also Stephenson, 1944).

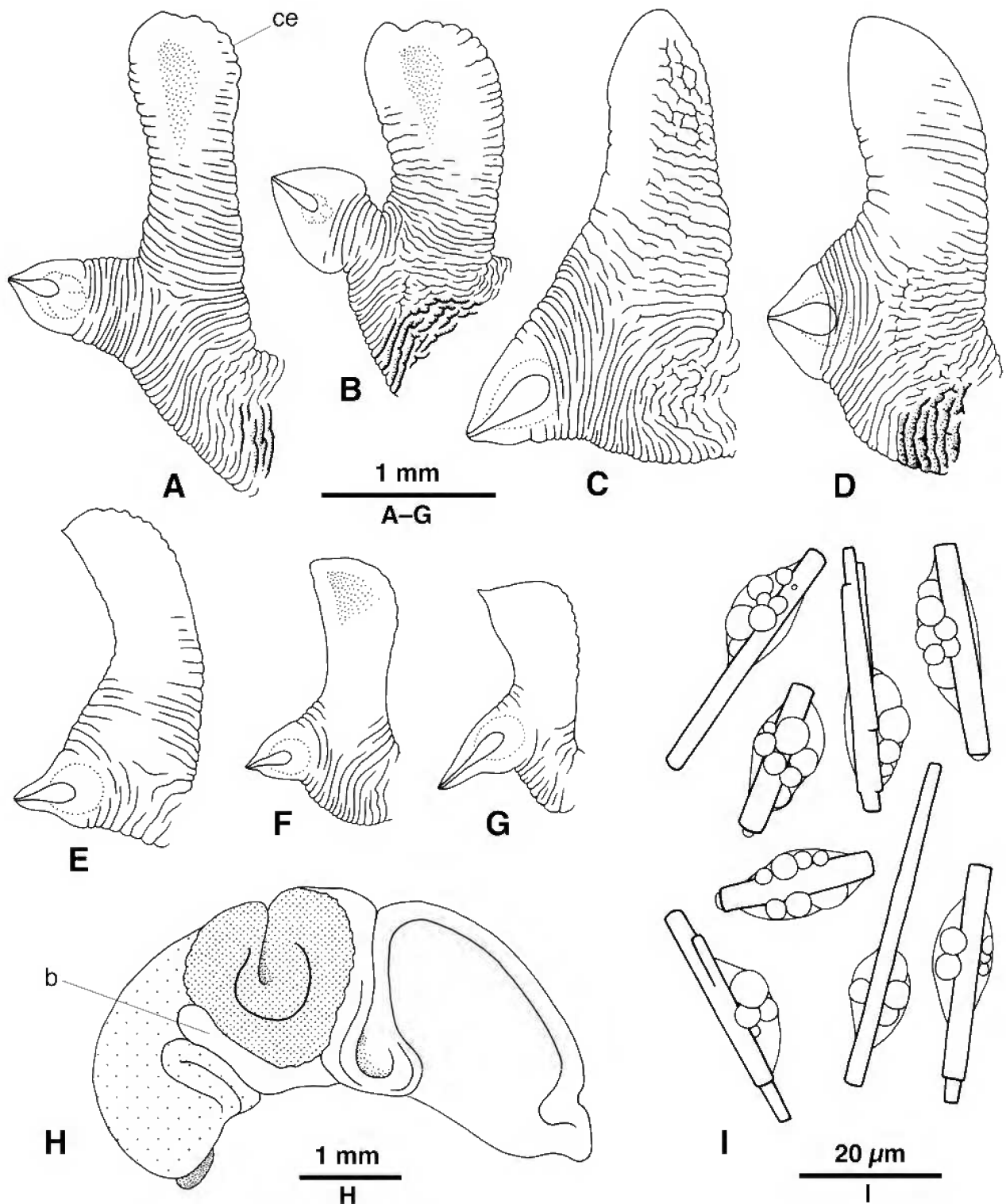


Fig. 20. *Afrolittorina knysnaensis*: (A–G) Penes. (H) Pallial oviduct. (I) Paraspermatozoa from one specimen. (A,B,I) Munster, South Africa (BMNH 20030434). (C,D,H) Oudekraal, South Africa (BMNH 20030435). (E) Knysna Head, South Africa (BMNH 20030436). (F) Port Edward, South Africa (BMNH 20030437). (G) Brent, South Africa (BMNH 20030438). Shell heights: (A) 6.5 mm, (B) 10.1 mm, (C,D) unknown, (E) 8.1 mm, (F) 6.5 mm, (G) 5.7 mm, (H) 14.9 mm. Abbreviations: (b) copulatory bursa; (ce) crimped edge of penial sperm groove. Shading conventions as in Fig. 3.

Remarks. Although they have been synonymized by several authors, the shells of *A. knysnaensis* and *A. africana* are almost always immediately separable by their coloration. That of *A. africana* is blue-grey, sometimes with faint fine tessellation of yellow-brown; that of *A. knysnaensis* is densely and minutely speckled with red-brown, with a broad

blackish peripheral band. Occasional pale or unpatterned shells of *A. knysnaensis* are more difficult to identify, but the periphery is usually more strongly angled than in *A. africana*. The operculum is more tightly wound in *A. knysnaensis* (i.e. higher opercular ratio). Anatomically, the penial filament of *A. knysnaensis* is more wrinkled, with a

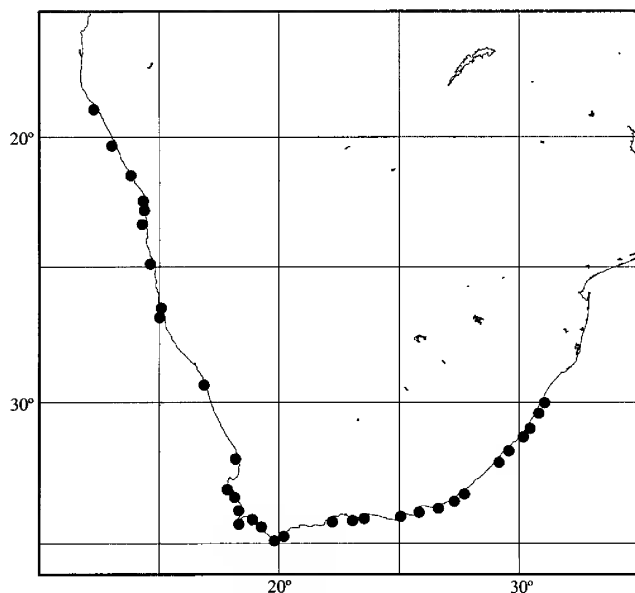


Fig. 21. Distribution of *Afrolittorina knysnaensis*.

crimped margin to the distal part of the sperm groove, the grey colour of the subepithelial glandular tissue within the filament is slight or absent, and the rod-bodies within the paraspermatozoa are much longer and project from the cells. No anatomical difference has been detected between the females of the two species. Both Rosewater (1970) and Hughes (1979) have noted that the margin of the mantle is pigmented in *A. africana* and not in *A. knysnaensis*, but this character is inconsistent and both pigmented and unpigmented states can be found frequently in both species.

Distribution maps give the impression of a broad overlap between the ranges of *A. knysnaensis* and *A. africana*, from False Bay to the vicinity of Durban. However, in a survey of the distribution of these species on the South African coast, Hughes (1979) found that *A. knysnaensis* was dominant at all sites as far north as East London, both species were common at Port St Johns, and only *A. africana* was common in Natal. *Afrolittorina knysnaensis* occurs alone on the Atlantic coast of southern Africa, under the influence of the cold Benguela Current, and is clearly a cool-temperate species, whereas *A. africana* shows a warm-temperate and subtropical distribution (Stephenson, 1944). The temperature relations of these two species have been studied by McQuaid & Scherman (1988), who showed that body temperatures of brown-shelled *A. knysnaensis* were 2–3°C higher than those of white-shelled *A. africana*, when both were attached by mucus to open rock surfaces on the shore in full sunlight (there was no difference when attached by the foot, because conductive heat gain overrode the effect of decreased radiant absorption by the paler shell). Behavioural observations also showed that *A. knysnaensis* was less tolerant of insolation than *A. africana*, for the former tended to occur in damp, shady pits in the rock rather than on open surfaces, at least when subjected to long periods of emersion during neap tides. These authors suggested that the lower tolerance of *A. knysnaensis* to heating by sunlight might explain its replacement by *A. africana* on the subtropical east coast of South Africa. There is an interesting parallel with the two species of *Austrolittorina* in New Zealand, where the brown *A. cincta* is more common in the south and the blue-white *A. antipodum* in

the north. In Australia, *Afrolittorina praetermissa* has a patterned or brown shell and is a cool-water species, whereas *Austrolittorina unifasciata* with a white shell extends along warm-temperate coasts. The pattern is repeated within *Austrolittorina araucana* on the west coast of South America, where entirely brown populations occur in the south and mixed brown and white populations in the north (Reid, 2002a). Climatic selection might account for all these trends. The importance of pale shells as a means of temperature regulation in intertidal gastropods has been reviewed by Vermeij (1973) and has also been recorded in some tropical littorinid species (Markel, 1971). McQuaid & Scherman (1988) found no evidence of visual selection on shell colour, but Hughes (1979) noted a correlation between the abundance of *Afrolittorina africana* and pale rocks, implying that visual selection might also be involved.

Two other littorinid species have been recorded from the temperate coast of southern Africa. *Littorina saxatilis* (Olivier, 1792) occurs at two sites, Langebaan and Knysna, among marsh grass and on stones in sheltered lagoons. Neither of the southern African *Afrolittorina* species can be found in this habitat. The shells of these populations of *L. saxatilis* are smooth, thin-walled, with well-rounded whorls and are variously coloured in shades of yellow and brown, usually with a coarsely marbled or tessellated pattern. Anatomically they are quite distinct and no confusion should occur (see Reid, 1996, for review). These colonies are apparently the basis for the records of “*Littorina punctata*” in South Africa by Barnard (1963; see Kilburn, 1972). Rosewater (1970) accepted Barnard’s records of “*L. punctata*” from South Africa and added others from Port Elizabeth; these may have been based on misidentification of *A. knysnaensis*, for *E. punctata* does not occur south of Namibia (Kilburn, 1972). It has recently been suggested that *Echinolittorina punctata* consists of a complex of three species (Reid, 2002b), of which the one in Namibia should be known as *Echinolittorina pulchella* (Dunker, 1845). Kilburn (1972) stated that the range of this species abuts that of *A. knysnaensis* at Rocky Point in Namibia, where both species occur together. Furthermore, he suggested that the presence of apparent intermediates (in shell pattern) to the south implied hybridization. It is true that shells of *E. pulchella* and of *A. knysnaensis* can be similar, but it is now clear that there are significant anatomical differences between the two. The pallial oviduct of *E. pulchella* contains only a single loop of the egg groove, in the albumen gland, and the penis shows a glandular disc in addition to the mamilliform gland. The colour pattern of *E. pulchella* is of relatively coarse tessellation of brown to black spots, aligned in oblique series on a pale ground, often appearing as a black shell with large white spots. In contrast, the shell of *A. knysnaensis* has a finely speckled brown pattern; this is visible on the base even in those that are almost black above the periphery, as is frequent in samples from Namibia.

Hughes (1979) mentioned and illustrated unusually elongated shells from Arniston (Fig. 19F). Some of these have been dissected and found to contain trematode parasites, which were presumably responsible for the distortion. Kilburn (1972) reported that the peripheral keel was more well developed in samples from wave-exposed shores, whereas it was said to be absent in estuarine shells, which were also found to be larger in size. The largest examples seen in the present study were from the Atlantic coast.

Afrolittorina praetermissa (May, 1909)

Figs. 17E,F, 22–24, 25C–E

- ?Littorina ziczac*.—Philippi, 1847: 162–163 (not *Trochus ziczac* Gmelin, 1791 = *Echinolittorina ziczac*; in part; includes *E. ziczac*; inclusion in synonymy based on locality Kangaroo Island).
- Littorina ziczac*.—Tenison Woods, 1879: 69 (not Gmelin, 1791; in part; includes *E. ziczac*).
- Littorina philippii*.—Angas, 1865: 172 [not *Littorina philippii* Carpenter, 1857 = *Echinolittorina apicina* (Menke, 1851)]. Tenison Woods, 1878: 36 (as *philippi*; not Carpenter, 1857). Gatliff, 1887: 60 (as *philippii*; not Carpenter, 1857).
- Littorina undulata*.—Angas, 1865: 172 (not Gray, 1839 = *Littoraria undulata*). Tenison Woods, 1878: 36 (not Gray, 1839).
- Littorina paludinella*.—Tenison Woods, 1878: 36 (not Reeve, 1857; see Hedley, 1913; Ponder & Rosewater, 1979). Gatliff, 1887: 60 (not Reeve, 1857). Pritchard & Gatliff, 1902: 92 (not Reeve, 1857).
- Melarapha paludinella*.—Macpherson & Gabriel, 1962: 89 (not Reeve, 1857).
- Littorina caerulescens*.—Tenison Woods, 1879: 65–72 (as *coerulescens*; not *Turbo caerulescens* Lamarck, 1822 = *Melarapha neritoides*; in part; includes *A. africana*, *Austrolittorina unifasciata*, *A. antipodum*, *Littoraria mauritiana*, *M. neritoides*).
- Littorina unifasciata*.—Haacke, 1885: 504–505 (not Gray, 1826; in part, includes *Austrolittorina unifasciata*).
- Littorina mauritiana*.—Tate & May, 1901: 389 (not *Phasianella mauritiana* Lamarck, 1822 = *Littoraria mauritiana*; in part; includes *Austrolittorina unifasciata*).
- Littorina novaezealandiae* “Reeve” Pritchard & Gatliff, 1902: 91 (unjustified emendation of *Littorina novaezealandiae* Reeve, 1857; not Reeve, 1857 = *Echinolittorina novaezealandiae*; in part; includes *E. novaezealandiae*).
- Littorina praetermissa* May, 1909: 57, pl. 6, fig. 3 (Tasmania; holotype TMAG E353/7694, fig. 22G, seen; 4 possible paratypes MCZ 23099, seen).
- Melarapha praetermissa*.—Hedley, 1913: 1913 (as *Melaraphe*). May, 1921: 47. May, 1923: 49, pl. 22, fig. 18. Cotton & Godfrey, 1938: 10. Macpherson & Chapple, 1951: 118 (as *Melaraphe*). Kershaw, 1955: 307 (as *Melaraphe*).
- Littorina praetermissa*.—Guiler, 1958: 139. Wilson & Gillett, 1979: 52, pl. 8, fig. 8, 8a.
- Melarapha praetermissa*.—McMichael, 1959: 27. Iredale & McMichael, 1962: 38. Macpherson & Gabriel, 1962: 87–88, fig. 116.
- Littorina (Littoraria) praetermissa*.—Rosewater, 1970: 423, 445–446, pl. 325, figs. 26, 27, pl. 343, pl. 344, fig. A (radula), B (penis), pl. 345 (distribution).
- Littorina (Austrolittorina) praetermissa*.—Ponder & Rosewater, 1979: 775, pl. 3, fig. 3 (penis). Ludbrook & Gowlett-Holmes, 1989: 564–565. Wilson, 1993: 146, pl. 18, fig. 4a,b.
- Nodilittorina praetermissa*.—Bandel & Kadolsky, 1982: 3.
- Nodilittorina (?Nodilittorina) praetermissa*.—Reid, 1989: 100.
- Nodilittorina (Austrolittorina) praetermissa*.—Reid, 2002a: 154.
- Afrolittorina praetermissa*.—Williams *et al.*, 2003.

Taxonomic history. This species is common on the shores of southern Australia and Tasmania, so it is remarkable that it was not named until 1909. Before this, it was variously misidentified. The earliest apparent reference to the species is Philippi’s (1847) record of *Littorina ziczac* from Kangaroo Island in South Australia, collected by Harvey; Philippi’s figure 13 may be this species, but no locality was given. The use of the name *Littorina philippii* (Angas, 1865; Tenison Woods, 1878; Gatliff, 1887) is surprising, because this taxon was described from Mexico.

Several authors used the name *Littorina paludinella* for a juvenile form of this species that is a small, low-spired

shell of brown colour with a pale basal band (Tenison Woods, 1878; Gatliff, 1887; Pritchard & Gatliff, 1902; Macpherson & Gabriel, 1962). However, Hedley (1913) examined the types of Reeve’s species and found that they were a hydrobiid from Tasmania, as subsequently confirmed (Ponder & Rosewater, 1979; Ponder *et al.*, 1993).

This species has sometimes been considered as a striped form of the sympatric *Austrolittorina unifasciata* (Tenison Woods, 1879; Haacke, 1885; Tate & May, 1901; see Taxonomic History of *A. unifasciata*).

Diagnosis. Shell moderately large, patulous to high-turbinate, periphery rounded, usually sculptured with incised spiral lines; pale, with brown tessellated or marbled pattern. Penis with rounded, slightly swollen filament; mamilliform gland and glandular disc on base. Pallial oviduct with three consecutive loops of egg groove, in albumen gland, capsule gland and in terminal portion of oviduct.

Material examined. 64 lots (45 AMS, 7 USNM, 9 BMNH, 1 ZMA, 1 MNHNP, 1 NMW), including 8 penes, 4 sperm samples, 6 pallial oviducts, 3 radulae.

Shell (Figs. 22, 25C–E). Mature shell height 8.2–19.4 mm (down to 3 mm, Nwe, 1974). Shape patulous to high-turbinate (H/B = 1.13–1.60; SH = 1.20–1.95); spire outline slightly concave; whorls well rounded, suture distinct, periphery rounded or slightly angled; moderately solid. Columella pillar straight to slightly concave; columella excavated; sometimes a slight pseudumbilicus (frequent in juveniles); eroded parietal area absent. Sculpture of 13–16 primary spiral grooves above periphery, remaining as approximately equidistant incised lines, continuing faintly on base; periphery sometimes marked by a slightly raised rib; secondary division occasionally increases spiral lines to up to 22 above periphery on last whorl; prominence of spiral lines varies, juveniles are usually smooth and lines often become obsolete on last whorl; microscopically, surface is shiny with only faint spiral microstriae; spire usually eroded; growth lines may be strong at end of last whorl. Protoconch rarely preserved, about 0.34 mm diameter, 3 whorls. Colour whitish, cream or pale blue-grey; pale grey brown to dark brown pattern, finely tessellated or marbled, often aligned to form oblique axial stripes or zigzags, occasionally spiral lines; juveniles dark brown with white spiral band on base, pattern of additional pale bands and marbling appearing only on and after whorl 3 of teleoconch; aperture dark brown with basal white band.

Animal. Head and sides of foot black; tentacles with two broad longitudinal black stripes, fusing distally, sometimes completely fused to give black tentacles. Opercular ratio 0.46–0.52. Penis (Fig. 23A–E): filament 0.4–0.5 total length of penis, bluntly rounded, smooth, slightly swollen; sperm groove open to filament tip; single large mamilliform gland and adjacent smaller lobe of penial glandular disc borne together on lateral branch of base; penis unpigmented; penis regresses to a stub outside May–October breeding season (Nwe, 1974). Euspermatozoa 61–66 µm; paraspermatozoa (Fig. 23J,K) spherical to oval, 13–21 µm diameter, containing large spherical granules and one (or up to 6) small, rectangular or irregular rod-bodies that are hexagonal in section and do not project from cell. Pallial oviduct (Fig. 23F,G) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, opaque pink, within which central portion

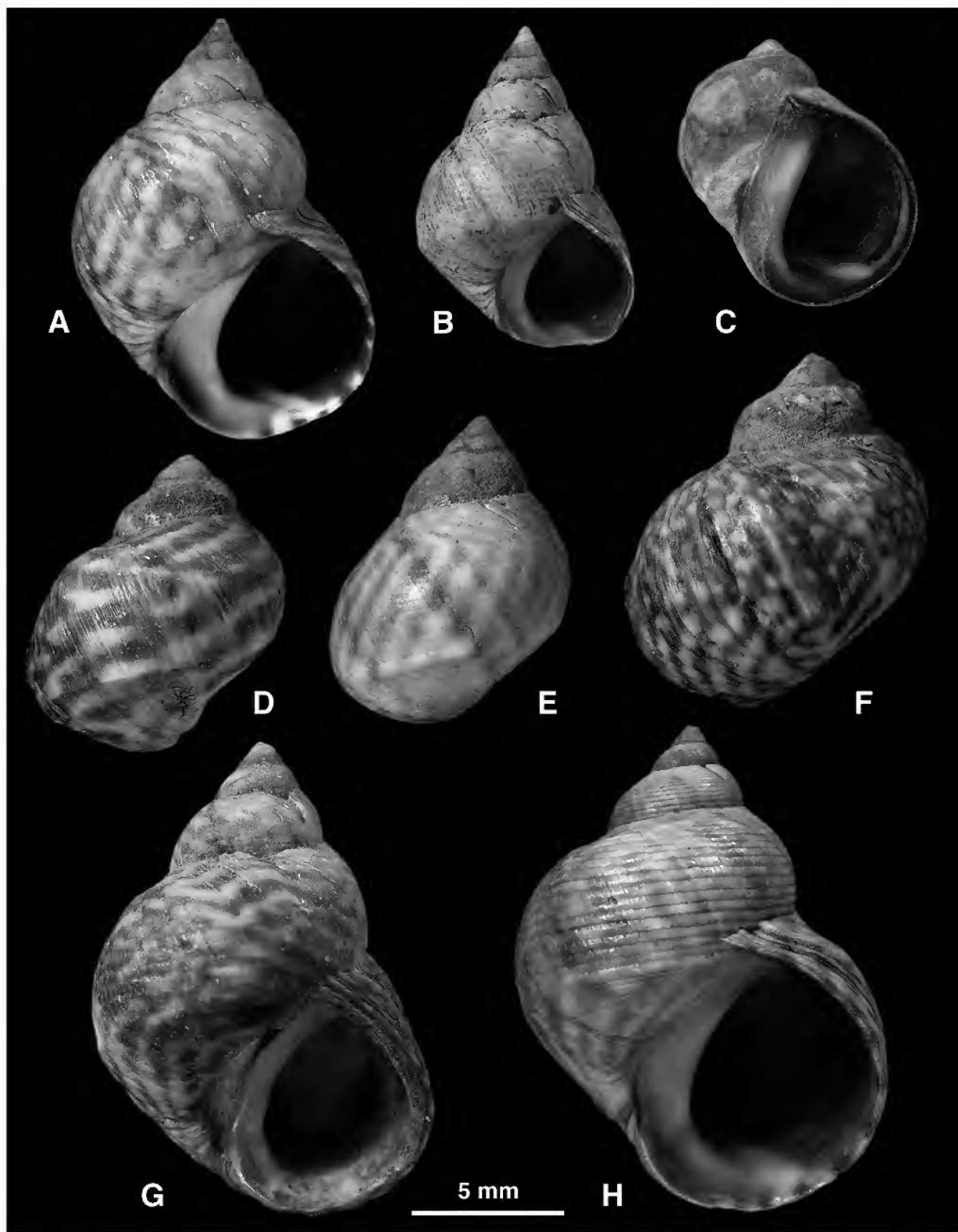


Fig. 22. *Afrolittorina praetermissa*: (A) southern Tasmania, Australia (BMNH 20030439). (B) Cape Sorrell, Tasmania, Australia (AMS C387215). (C) Lion Island, Recherche Archipelago, Western Australia (AMS C386849). (D,F) Burnie, Tasmania, Australia (AMS C387214). (E) Shelly Beach, Phillip Island, Victoria, Australia (BMNH 20030440). (G) Holotype of *Littorina praetermissa* May, 1909 (TMAG E353/7694). (H) London Bridge, near Port Campbell, Victoria, Australia (AMS C387216).

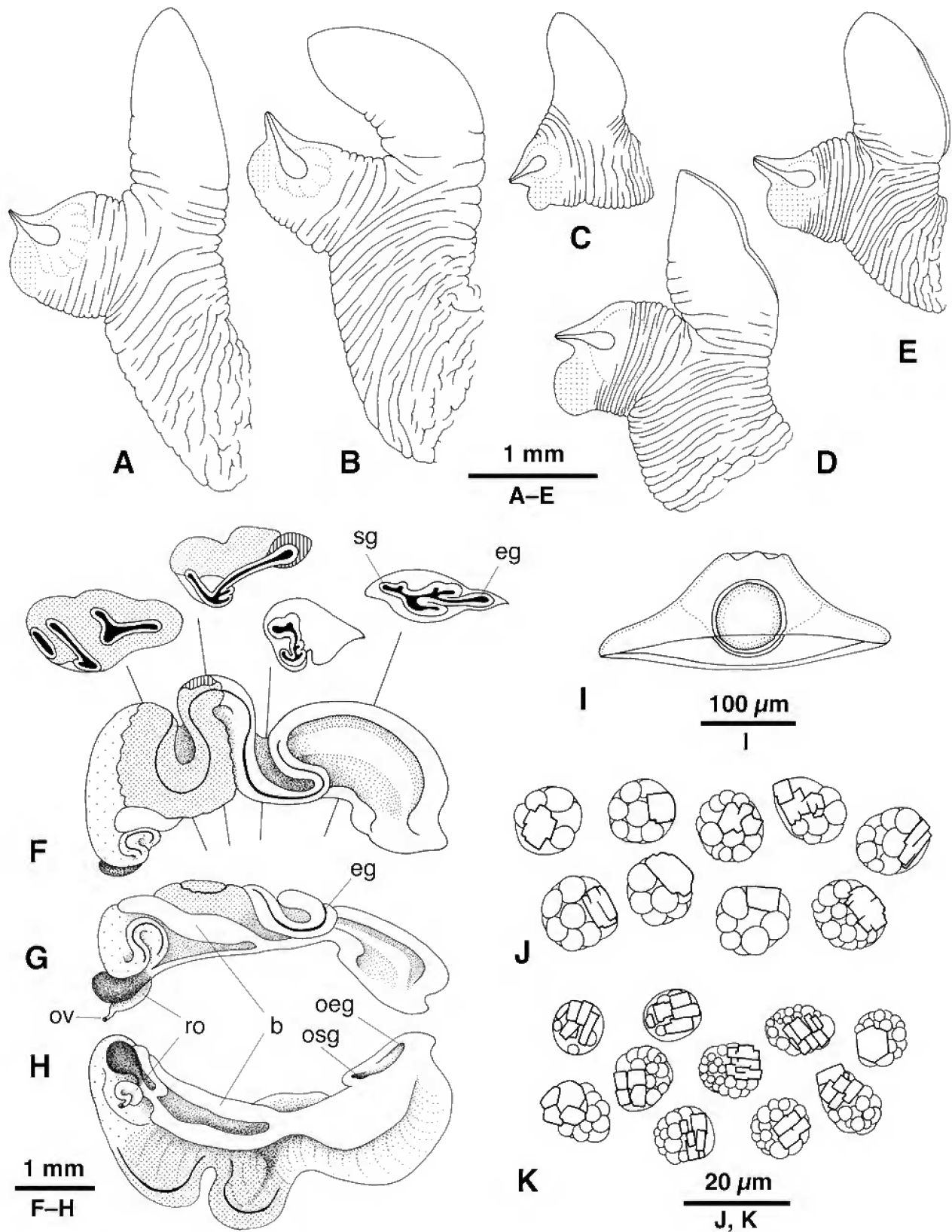


Fig. 23. *Afrolittorina praetermissa*: (A–E) Penes. (F–G) Pallial oviduct from slightly immature specimen (glands are less swollen, so that spiral route of egg groove is clearly visible; mature oviduct resembles Fig. 19H in (F) lateral, (G) ventral, and (H) medial views. (I) Egg capsule (after Nwe, 1974). (J, K) Paraspermatozoa from two specimens. (A, B, F–H, J) Pirates Bay, Eaglehawk Neck, Tasmania, Australia (BMNH 20030441). (E, K) Blackmans Bay, Tasmania, Australia (BMNH 20030442). (D) Southport, Tasmania, Australia (BMNH 20030443). (I) Gulf St Vincent, South Australia. Shell heights: (A) 9.7 mm, (B) 10.3 mm, (C) 8.5 mm, (D) 10.8 mm, (E) 8.2 mm, (F–H) 12.5 mm. Abbreviations: (b) copulatory bursa; (eg) egg groove (visible by transparency as line of black pigment); (oeg) anterior opening of egg groove; (osg) anterior opening of sperm groove; (ov) cut ovarian oviduct (from ovary); (ro) renal oviduct. Shading conventions as in Fig. 3.

adjacent to egg groove and distal portion are differentiated as reddish translucent capsule gland; additional simple loop of glandular material between capsule gland and terminal straight portion; copulatory bursa separates in a posterior position and continues back to overlay albumen gland.

Spawn and development. Spawn (Fig. 23I) a transparent pelagic capsule 240–300 µm diameter containing a single ovum 80 µm diameter, capsule hat-shaped with waved concentric ring on crown and wide peripheral brim; development planktotrophic; females mature July–September in vicinity of Adelaide (Nwe, 1974). Pelagic spawn also observed by F. Murray (quoted in Pilkington, 1971).

Radula (Fig. 17E,F). Relative radular length 4.1–7.6. Rachidian: length/width 1.16–1.53; major cusp elongate, rounded at tip. Lateral and inner marginal: major cusps large, elongate to rectangular, rounded to truncate at tip. Outer marginal: 7–8 cusps (12, Nwe, 1974).

Habitat. In South Australia (Womersley & Edmonds, 1958; Nwe, 1974) and Victoria (Bennett & Pope, 1953) *A. praetermissa* is less common than the abundant *Austrolittorina unifasciata*; it occupies the lower littoral fringe (overlapping with, but lower than *A. unifasciata*) and favours more sheltered habitats, where it is found on a variety of hard substrates including wooden piers, and occurs in shaded crevices. Juveniles occur lower, in the upper barnacles zone (Bennett & Pope, 1953; Ponder & Rosewater, 1979). Reports of the habitat of *A. praetermissa* in Tasmania confirm that it occurs slightly lower on the shore than *A. unifasciata* and often in more cryptic microhabitats; however, it is said to predominate at wave-exposed sites, especially on cliffs with intense spray (Guiler, 1952b,c; Bennett & Pope, 1960; Newman, 1994; contrary report by Guiler, 1955, suggests possible confusion of names of taxa). Of these two, only *A. praetermissa* occurs on the cold, strongly exposed west coast of Tasmania, where it is found over the whole rock surface (Bennett & Pope, 1960).

Range (Fig. 24). Southern Australia, from southwestern Western Australia to Tasmania and southern New South Wales. The main centre of distribution of this species is from the Eyre Peninsula (SA) along the coastline of Victoria to Wilsons Promontory, the islands of Bass Strait and the entire

coastline of Tasmania. Several records are outside this range, all of which are of small numbers of juvenile or small shells. To the west, it is recorded from Point Sinclair, SA (32°06'S 133°00'E, AMS C390493, juveniles); Lion Island, Recherche Archipelago, WA (33°53'S 122°01'E, AMS C69337, 7 specimens, max. H = 8.5 mm); near Esperance, WA (33°51'S 121°53'E, AMS C390482 and C390490, 1 and 4 juveniles); Nine-Mile Beach, Esperance, WA (BMNH 20030447, 10 specimens, max. H = 4.8 mm); Hopetoun, WA (33°57'S 120°07'E, AMS C390489, 2 juveniles); south of Cowaramup, WA (33°52'S 115°05'E, AMS C390491, 1 juvenile). The species has not previously been recorded from Western Australia (unless the record of *Melarhapha undulata* from King George Sound by Hedley, 1916, might possibly have been *A. praetermissa*). A recent record from the vicinity of Perth, WA (A. Cummings, pers. comm.; figured by Schneider, 2003: fig. 1) is based on a worn specimen of *Echinolittorina vidua* (Gould, 1859). To the east the two records from southern NSW are from Twofold Bay (37°05'S 149°54'E, AMS C356463, 2 juveniles) and Burrill Lake (35°23'S 150°27'E, AMS C427919, 1 juvenile). This confirms the occurrence in NSW recorded by Bennett & Pope (1960) and Macpherson & Gabriel (1962, as *Melarapha paludinella*), although this was denied by Ponder & Rosewater (1979).

Remarks. This species shows considerable variation in shape, from low-spined and patulous (Fig. 22C) to high-turbinate (Fig. 22B); possible correlation of this variation with habitat has not yet been investigated. Small shells are dark brown with a pale basal band (Fig. 25C–E) and do not show the typical marbled pattern of the adults; this has led to some taxonomic confusion (see Taxonomic History above). These juveniles should not be confused with any other species; at a similar size (3–4 mm) the shells of the sympatric *Austrolittorina unifasciata* are blue-grey with fine brown spiral lines (Fig. 25A,B). In southern NSW the distribution just overlaps that of *Afrolittorina acutispira*, but that small species has a more tall-spined shell (Fig. 25G–N). Adult shells of *A. praetermissa* can usually be distinguished from *Austrolittorina unifasciata* by the presence of a brown pattern of marbling, tessellation or stripes on the shell of the former; the penial filament is shorter in *A. praetermissa* and the pallial oviduct shows three consecutive loops of the egg groove, not two.

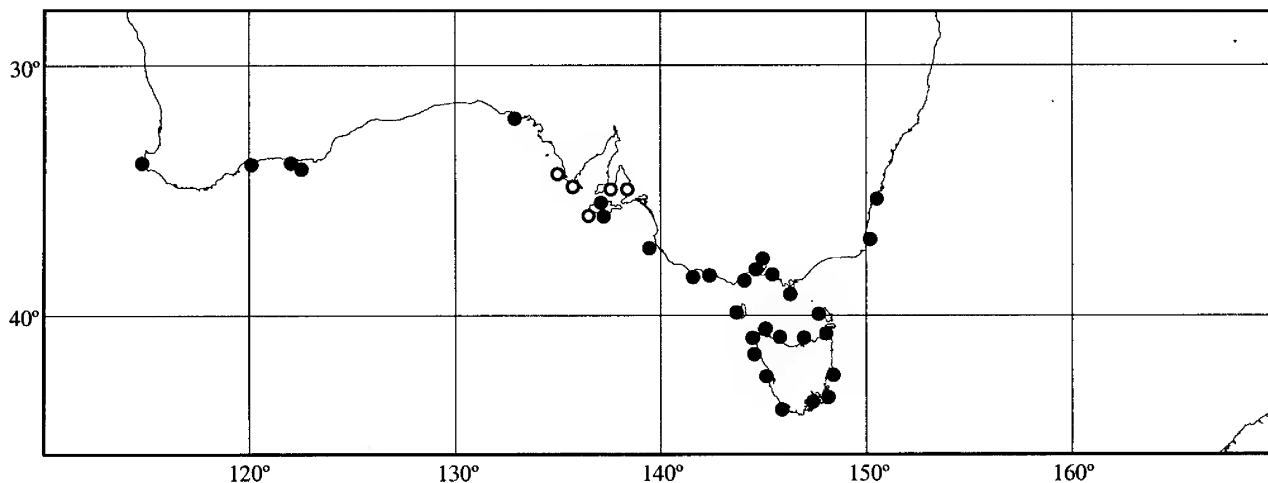


Fig. 24. Distribution of *Afrolittorina praetermissa*. Open circles are distribution records from Nwe (1974).

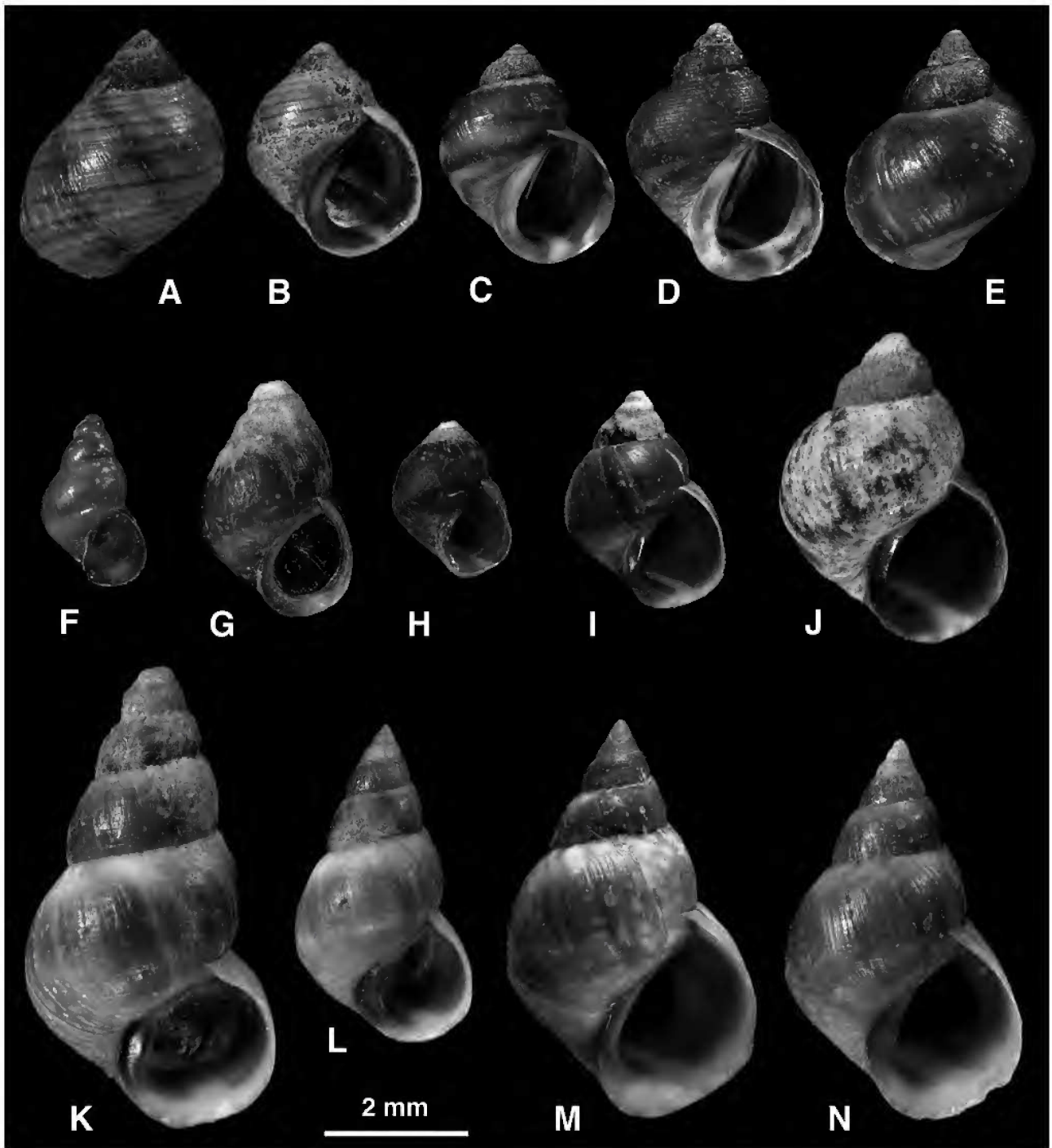


Fig. 25. Small and juvenile Australian Littorinidae. (A,B) *Austrolittorina unifasciata*, juvenile; Mylestom, NSW, Australia (BMNH 20030400). (C–E) *Afrolittorina praetermissa*, juvenile; Norman Bay, Wilsons Promontory, Victoria, Australia (AMS C387247). (F) *Laevilittorina mariae*; Merricks, Western Port Bay, Victoria, Australia (AMS C166157). (G–N) *Afrolittorina acutispira*. (G) Syntype of *Littorina infans* E.A. Smith, 1892; Port Jackson, NSW, Australia (BMNH 1891.11.6.226). (H) South side of Caloundra Gead, Queensland (AMS C387248). (I,J) Mrs Macquaries Point, Port Jackson, NSW, Australia (BMNH 20030444). (K) Green Point, Watsons Bay, Port Jackson, NSW, Australia (AMS C008909). (L) Lectotype of *Littorina acutispira* E.A. Smith, 1892; Port Jackson, NSW, Australia (BMNH 1891.11.6.216). (M) Green Point, Watsons Bay, Port Jackson, NSW, Australia (BMNH 20030445). (N) Green Point, Watsons Bay, Port Jackson, NSW, Australia (AMS C357030).

The present records extend the known range of this species into WA and NSW for the first time, but these outlying records are all of small or juvenile shells and might represent occasional long-distance dispersal events that do not result in permanent colonization.

This species is a characteristic member of the cool-

temperate component of the southern Australian fauna (Bennett & Pope, 1953, 1960). Its predominance on wave-exposed shores in Tasmania, but preference for cryptic microhabitats on sheltered shores in Victoria and South Australia, might suggest habitat restriction in the warmer parts of its range.

Molecular data have shown that *A. praetermissa* and *A. acutispira* are sister species, with an estimated time of more than 10 million years since divergence (Williams *et al.*, 2003). Molecular estimates of age in the absence of fossil calibration are approximate, but this estimate appears to rule out divergence to the east and west of Tasmania during Pleistocene low sea-level stands when Bass Strait was dry (for examples of this common pattern see Wilson & Allen, 1987). The almost complete allopatry between this pair, despite the old divergence time, is noteworthy. As in other sister-species pairs of southern littorinines that occupy the same land masses (*Austrolittorina antipodum* and *A. cincta* in New Zealand; *Afrolittorina africana* and *A. knysnaensis* in southern Africa), the ecological and geographical separation between these two species appears to be along an axis of temperature.

Afrolittorina acutispira (E.A. Smith, 1892)

Figs. 17G,H, 25G–N, 26, 27

Littorina acutispira E.A. Smith, 1892: 487–488, pl. 40, fig. 3 (Green Point, Watson Bay, Port Jackson, New South Wales; also Parsley Bay, Port Jackson; lectotype (Rosewater, 1970: 452) BMNH 1891.11.6.216 (fig. 25L; label: “Port Jackson”), 13 paralectotypes BMNH 1891.11.6.217–225 (“Port Jackson”), 47 paralectotypes BMNH 1886.7.26.102–111 (“Parsley Bay”), all seen).

Melarthaphe acutispira.—Hedley, 1918: M51.

Melarapha acutispira.—Iredale & McMichael, 1962: 38.

Littorina (?*Littoraria*) *acutispira*.—Rosewater, 1970: 423, 451–452, pl. 349, fig. 3, pl. 350 (distribution), pl. 351, fig. 1.

Littorina (*Austrolittorina*) *acutispira*.—Ponder & Rosewater, 1979: 773–774, pl. 1, figs. 1–3. Wilson, 1993: 146, textfig.

Nodilittorina acutispira.—Bandel & Kadolsky, 1982: 3. Jansen, 1995: 31, fig. 96.

Nodilittorina (?*Nodilittorina*) *acutispira*.—Reid, 1989: 99.

Nodilittorina (*Austrolittorina*) *acutispira*.—Reid, 2002a: 154.

Afrolittorina acutispira.—Williams *et al.*, 2003.

Littorina infans E.A. Smith, 1892: 488, pl. 40, fig. 4 (Green Point, Watson Bay, Port Jackson [New South Wales]); 14 syntypes BMNH 1891.11.6.226–235 (Fig. 25G), seen).

Melarthaphe infans.—Hedley, 1918: M51. Dakin, 1960: 248 (as *Melarapha*).

Melarapha infans.—Iredale & McMichael, 1962: 38.

Littorina (?*Littoraria*) *infans*.—Rosewater, 1970: 423, 452, pl. 351, fig. 2.

Taxonomic history. Smith (1892) named this species twice in the same publication, using the name *Littorina acutispira* for larger elongate shells and *L. infans* for smaller examples with eroded spires. Owing to their small size, both taxa were neglected by subsequent workers. Rosewater (1970) retained them as separate species. As first revisers, Ponder & Rosewater (1979) established the valid name.

Diagnosis. Shell small, tall-spined, smooth; pale, with brown tessellated or marbled pattern. Penis with rounded, swollen filament; mamilliform gland on narrow lateral branch of base. Pallial oviduct with three consecutive loops of egg groove, in albumen gland, capsule gland and in terminal portion of oviduct.

Material examined. 56 lots (45 AMS, 2 USNM, 9 BMNH), incl. 9 penes, 2 sperm samples, 10 pallial oviducts, 4 radulae.

Shell (Fig. 25G–N). Mature shell height 2–7.0 mm. Shape high-turbinate to tall-spined (H/B = 1.38–1.84; SH = 1.65–2.32), but may appear almost globular if spire strongly eroded; spire outline straight; whorls rounded, suture distinct; periphery rounded or slightly angled; small shells translucent, becoming solid. Columella pillar short, straight

to slightly concave; columella slightly excavated; sometimes a slight pseudoumbilicus; eroded parietal area absent. Sculpture frequently microscopically smooth, but larger shells may have 11–22 spiral striae or impressed lines on last whorl, striae rarely visible on spire; surface shiny, microstriae absent; growth lines insignificant. Protoconch rarely preserved, 0.29–0.34 mm diameter, 3 whorls, terminated by sinusigera ridge, sculpture unclear. Colour: juveniles brown with spiral white band on base; larger shells cream to brown, usually with darker grey or grey-brown zone from periphery to near suture, entire surface with fine tessellation or marbling of white and pale brown, pattern not highly regular nor aligned into axial stripes, base usually paler; aperture dark brown with basal white band.

Animal. Head and sides of foot grey to black; pigmentation of tentacles varies, may be unpigmented, or with single longitudinal black line or two broad black lines. Opercular ratio 0.45–0.52. Penis (Fig. 26A–E): filament half total length of penis, swollen with subepithelial glandular tissue, bluntly rounded; sperm groove opens subterminally; single mamilliform gland (and probably also a small patch of subepithelial glandular tissue corresponding to reduced glandular disc, on ventral side of mamilliform gland, visible in histological section only) borne on narrow lateral branch of base; penis unpigmented. Euspermatozoa length unknown; paraspermatozoa (Fig. 26H,I) elongate-oval, 20–30 µm long, containing single (rarely 2) narrow rod piece, sometimes slightly projecting, cell packed with large spherical granules and one larger oval granule. Pallial oviduct (Fig. 26F,G) with simple loop of albumen gland, followed by large capsule gland forming a loop (although loop is difficult to distinguish except in juveniles where gland is less swollen); additional simple loop of glandular material between capsule gland and terminal straight portion; copulatory bursa separates in a posterior position and continues back to overlay capsule gland.

Spawn and development. Pelagic egg capsules 169–188 µm diameter (similar to those of *Austrolittorina antipodum* illustrated by Pilkington, 1971), containing single eggs 75–93 µm diameter; development planktotrophic; breeding season October/November to March/April (Underwood & McFadyen, 1983).

Radula (Fig. 17G,H). Relative radular length 1.21–1.67. Rachidian: length/width 1.12–1.47; central cusp long, sharply pointed, smaller pointed cusp on either side. Lateral: small inner cusp and three well-developed pointed cusps. Inner marginal: four well-developed pointed cusps. Outer marginal: 6–9 cusps.

Habitat. This species is one of the most abundant molluscs on the rock platforms of New South Wales (Dakin, 1960; Underwood, 1981), although often overlooked because of its small size. In a detailed study of its population dynamics Underwood & McFadyen (1983) recorded densities of up to 70000 m⁻² at the highest levels of the littorinid zone on platforms in Botany Bay. The highest densities were found on an exposed shore, in areas where barnacles provided crevices for protection from waves. On a sheltered shore, most snails were found in shallow pools with *Enteromorpha*. In southern Queensland the species is also found among barnacles and in shallow pools (Johnston, 1917), and occupies a zone between high water of neap tides and mean sea level (Endean *et al.*, 1956), below that of the larger littorinids.

Range (Fig. 27). Southeastern Australia from New South Wales

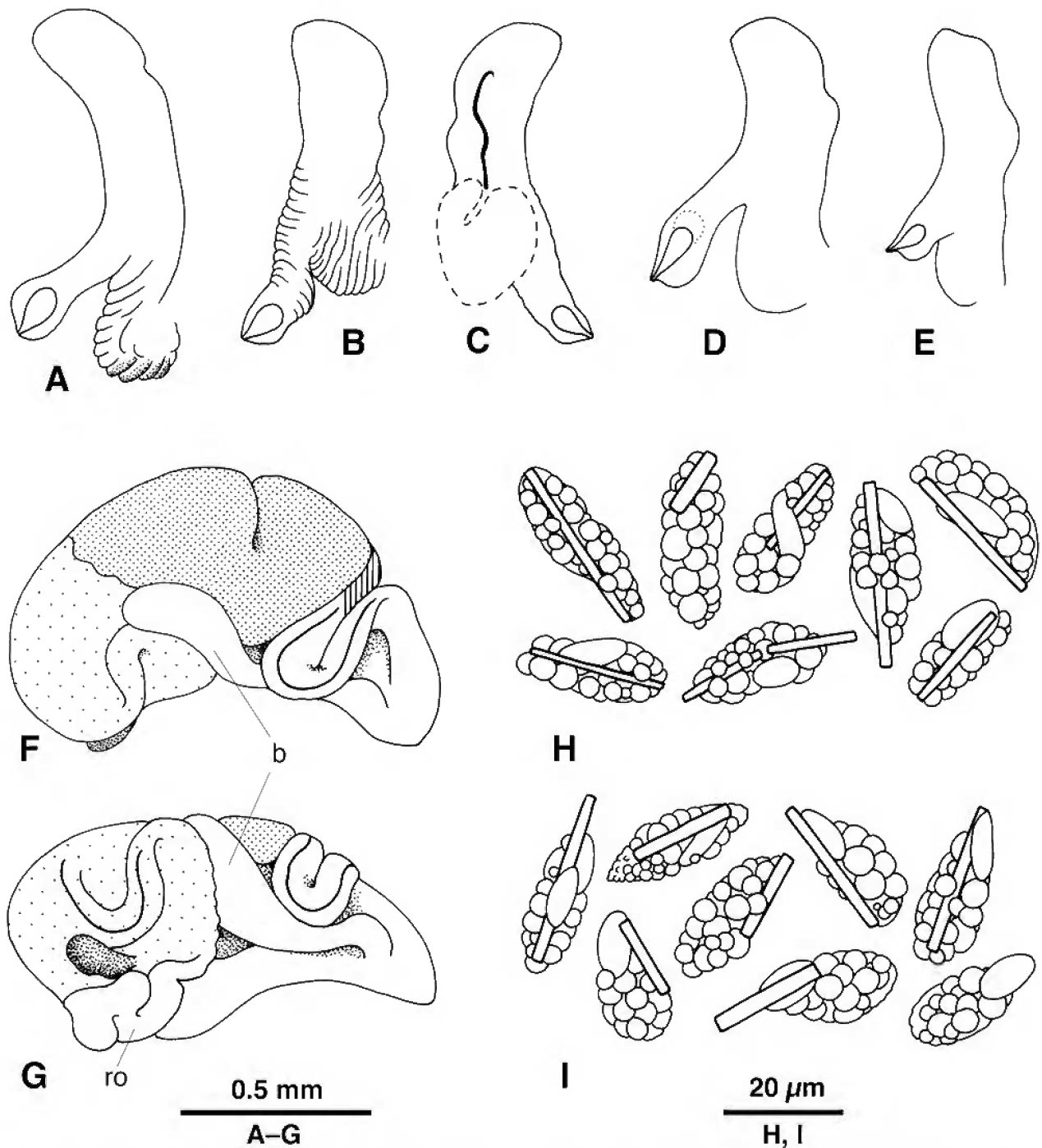


Fig. 26. *Afrolittorina acutispira*: (A–E) Penes (B) and (C) are lateral and medial view of same specimen). (F, G) Pallial oviduct of one specimen in (F) lateral and (G) ventral view. (H, I) Paraspermatozoa from two specimens. (A–C, F–I) Fairlight, North Harbour, Sydney, NSW, Australia (BMNH 20030446). (D, E) Bottle and Glass Rocks, Sydney Harbour, NSW, Australia (AMS C357850). Shell heights: (A) 3.9 mm, (B, C) 3.5 mm, (D) 3.3 mm, (E) 2.6 mm, (F) G, 4.0 mm. Abbreviations: (b) copulatory bursa; (ro) renal oviduct. Shading conventions as in Fig. 3.

to southern Queensland. This species is frequent along the entire coastline of New South Wales, the southernmost record being from Eden (37°04'S 149°54'E, AMS C357489). In Queensland it is common as far north as Noosa Heads (26°23'S 153°09'E, AMS C388093) and there are isolated records further north from Pialba, Hervey Bay (25°18'S 152°50'E, AMS C390527), Facing Island (23°49'S 151°22'E, AMS C390516), Gladstone (23°51'S 151°15'E, AMS C018502) and Yeppoon (23°9'S 150°46'E, AMS C390525). A record based on a single shell from Hayman Island (AMS C390526) requires verification.

Remarks. *Afrolittorina acutispira* is an abundant species throughout most of its range. Its small size and tall-spined, patterned shell readily distinguish it from the sympatric *Austrolittorina unifasciata*, and its habitat in pools, among algae and in barnacles is generally lower on the shore. At a similar size, juvenile shells of *Austrolittorina unifasciata* are blue-grey, with fine brown spiral lines (Fig. 25A, B). Juveniles of *Afrolittorina praetermissa* are brown with a basal pale band, like those of *A. acutispira*, but are broader (Fig. 25C–E), and that species is rare in southern New South Wales.

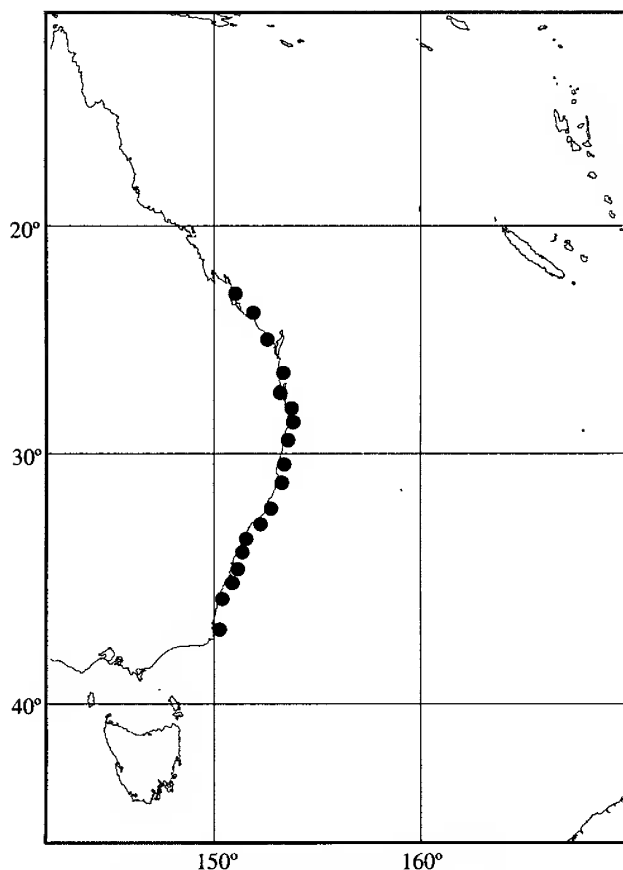


Fig. 27. Distribution of *Afrolittorina acutispira*.

In the southern parts of its range, *L. acutispira* could be confused with *Laevillittorina mariae* (Tenison Woods, 1876), which occurs among algae on littoral rock platforms, although it is uncommon in New South Wales (Ponder & Rosewater, 1979). That species is of similar elongate shape, up to 3.4 mm in height, translucent brown in colour, with a pale spiral band on the base, however the columella is narrow and not excavated and the apex is bluntly rounded, with a bulbous protoconch 0.43 mm in diameter of 1.5 whorls (indicating nonplanktotrophic development) (Fig. 25F).

The radula looks markedly different from those of other species of *Afrolittorina*, *Nodilittorina* and *Austrolittorina*, owing to the more equal size and sharply pointed tips of all cusps. However, these characteristics are typical of both juveniles and small species in other littorinine genera, including *Peasiella* (Reid & Mak, 1998), *Littorina* (Reid, 1996) and *Echinolittorina* (Reid, 2002a, as *Nodilittorina*), and are therefore interpreted as an allometric consequence of small size, perhaps connected with a different diet or feeding mechanism in small snails.

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References

- Abbott, R.T., 1954. Review of the Atlantic periwinkles, *Nodilittorina*, *Echininus*, and *Tectarius*. *Proceedings of the United States National Museum* 103: 449–464.
- Adams, H., & A. Adams, 1853–1858. *The Genera of Recent Mollusca; Arranged according to their Organization*. London: John van Voorst.
- Allan, J., 1950. *Australian Shells*. Melbourne: Georgian House.
- Angas, G.F., 1865. On the marine molluscan fauna of the province of South Australia: with a list of all the species known up to the present time; together with remarks on their habitats and distribution, etc. *Proceedings of the Zoological Society of London* 1865: 155–190, 643–657.
- Angas, G.F., 1867. A list of species of marine Mollusca found in Port Jackson Harbour, New South Wales, and on the adjacent coasts, with notes on their habits, &c.—Part I. *Proceedings of the Zoological Society of London* 1867: 185–233.
- Bandel, K., & D. Kadolsky, 1982. Western Atlantic species of *Nodilittorina* (Gastropoda: Prosobranchia): comparative morphology and its functional, ecological, phylogenetic and taxonomic implications. *Veliger* 25: 1–42.
- Barnard, K.H., 1963. Contributions to the knowledge of South African marine Mollusca. Part III. Gastropoda: Prosobranchiata: Taenioglossa. *Annals of the South African Museum* 47: 1–199.
- Bartsch, P., 1915. Report on the Turton collection of South African marine mollusks, with additional notes on other South African shells contained in the United States National Museum. *Bulletin of the United States National Museum* 91: 1–305.
- Basingthwaight, G., & W. Foulds, 1985. The effect of wave action on the shell morphology of *Littorina unifasciata* Gray. *Journal of the Royal Society of Western Australia* 68: 9–12.
- Batham, E.J., 1956. Ecology of southern New Zealand sheltered rocky shore. *Transactions of the Royal Society of New Zealand* 84: 447–465.
- Batham, E.J., 1958. Ecology of southern New Zealand exposed rocky shore at Little Papanui, Otago Peninsula. *Transactions of the Royal Society of New Zealand* 85: 647–658.
- Bennett, I., & E. Pope, 1953. Intertidal zonation of the exposed rocky shores of Victoria, together with a rearrangement of the biogeographic provinces of temperate Australian shores. *Australian Journal of Marine and Freshwater Research* 4: 105–159.
- Bennett, I., & E.C. Pope, 1960. Intertidal zonation of the exposed rocky shores of Tasmania and its relationship with the rest of Australia. *Australian Journal of Marine and Freshwater Research* 11: 182–221.
- Bokenham, K.A.H., F.L. Neugebauer & T.A. Stephenson, 1938. The vertical distribution of certain intertidal marine gastropods in False Bay, with notes on the development of two of them. *Annals of the Natal Museum* 9: 113–137.
- Branch, G.M., & M.L. Branch, 1981. Experimental analysis of intraspecific competition in an intertidal gastropod *Littorina unifasciata*. *Australian Journal of Marine and Freshwater Research* 32: 573–589.
- Bright, K.M.F., 1938. The South African intertidal zone and its relation to ocean currents. III.—an area on the northern part of the West Coast. *Transactions of the Royal Society of South Africa* 26: 67–88.
- Britton, J.C., R.F. McMahon & J.W. Hart, 1991. Relationships between topography, substratum composition and surface temperature, and the spatial distribution of intertidal fauna on rocky shores of south-western Australia. In *The marine flora and fauna of Albany, Western Australia*, ed. F.E. Wells, D.I. Walker, H. Kirkman & R. Lethbridge, pp. 521–540. Perth: Western Australian Museum.
- Brook, F.J., 1998. The coastal molluscan fauna of the northern Kermadec Islands, southwest Pacific Ocean. *Journal of the Royal Society of New Zealand* 28: 185–233.

- Bruggen, A.C.van, 1992. Ferdinand Krauss and the Leiden Museum, with notes on his South African mollusc types. *Proceedings of the 9th International Malacological Congress*, Edinburgh, pp. 77–96.
- Bucknill, C.E.R., 1924. *Sea Shells of New Zealand*. Auckland: Whitcombe & Tombs.
- Chapman, M.G., 1986. Assessment of some controls in experimental transplants of intertidal gastropods. *Journal of Experimental Marine Biology and Ecology* 103: 181–201.
- Chapman, M.G., 1994a. Small-scale patterns of distribution and size-structure of the intertidal littorinid *Littorina unifasciata* (Gastropoda: Littorinidae) in New South Wales. *Australian Journal of Marine and Freshwater Research* 45: 635–652.
- Chapman, M.G., 1994b. Small- and broad-scale patterns of distribution of the upper-shore littorinid *Nodilittorina pyramidalis* in New South Wales. *Australian Journal of Ecology* 19: 83–95.
- Chapman, M.G., 1995a. Spatial patterns of shell shape of three species of co-existing littorinid snails in New South Wales, Australia. *Journal of Molluscan Studies* 61: 141–162.
- Chapman, M.G., 1995b. Aggregation of the littorinid snail *Littorina unifasciata* in New South Wales, Australia. *Marine Ecology Progress Series* 126: 191–202.
- Chapman, M.G., 1997. Relationships between shell shape, water reserves, survival and growth of highshore littorinids under experimental conditions in New South Wales, Australia. *Journal of Molluscan Studies* 63: 511–529.
- Chapman, M.G., 1998. Variability in trail-following and aggregation in *Nodilittorina unifasciata* Gray. *Journal of Experimental Marine Biology and Ecology* 224: 49–71.
- Chapman, M.G., 1999. Assessment of variability in responses of intertidal periwinkles to experimental transplantations. *Journal of Experimental Marine Biology and Ecology* 236: 171–190.
- Chapman, M.G., 2000. Variability of foraging in highshore habitats: dealing with unpredictability. *Hydrobiologia* 426: 75–87.
- Chapman, M.G., & A.J. Underwood, 1994. Dispersal of the intertidal snail, *Nodilittorina pyramidalis*, in response to the topographic complexity of the substratum. *Journal of Experimental Marine Biology and Ecology* 179: 145–169.
- Chapman, M.G., & A.J. Underwood, 1996. Influences of tidal conditions, temperature and desiccation on patterns of aggregation of the high-shore periwinkle, *Littorina unifasciata*, in New South Wales, Australia. *Journal of Experimental Marine Biology and Ecology* 196: 213–237.
- Chemnitz, J.H., 1781. *Neues Systematisches Conchylien-Cabinet*. Volume 5. Nürnberg.
- Chen, Y.S., & A.M.M. Richardson, 1987. Factors affecting the size structure of two populations of the intertidal periwinkle, *Nodilittorina unifasciata* (Gray, 1839), in the Derwent River, Tasmania. *Journal of Molluscan Studies* 53: 69–78.
- Clench, W.J., & R.T. Abbott, 1942. The genera *Tectarius* and *Echininus* in the Western Atlantic. *Johnsonia* 1: 1–4.
- Cooper, R.A., & P.R. Millener, 1993. The New Zealand Biota: historical background and new research. *Trends in Ecology and Evolution* 12: 429–433.
- Cotton, B.C., & F.K. Godfrey, 1938. A systematic list of the Gastropoda. The marine, freshwater, and land univalve Mollusca of south and central Australia. *Malacological Society of South Australia. Publication* 1: 1–44.
- Dakin, W.J., 1960. *Australian Seashores*. Edition 2. London: Angus & Robertson.
- Dakin, W.J., I. Bennett & E. Pope, 1948. A study of certain aspects of the ecology of the intertidal zone of the New South Wales coast. *Australian Journal of Scientific Research. Series B* 1: 176–230.
- Dautzenberg, P., 1932. Mollusques testacés marins de Madagascar. Supplément. *Journal de Conchyliologie* 76: 5–119.
- Delessert, B., 1841. *Recueil de Coquilles Décrites par Lamarck dans Son Histoire Naturelle des Animaux sans Vertèbres et Non Encore Figurées*. Paris.
- Dell, R.K., 1963. The littoral marine Mollusca of the Snares Islands. *Records of the Dominion Museum* 4: 221–229.
- Dellow, V., 1950. Inter-tidal ecology of Narrow Neck Reef, New Zealand. (Studies in inter-tidal zonation 3). *Pacific Science* 4: 355–374.
- Deshayes, G.P., 1839–1853. *Traité Élémentaire de Conchyliologie. Explication de Planches*. Paris: Victor Masson.
- Deshayes, G.P., 1843. *Histoire Naturelle des Animaux sans Vertèbres... par J.B.P.A. de Lamarck*. Edition 2. Volume 9. Paris: J.-B. Baillière.
- d'Orbigny, A., 1834–1847. *Voyage dans l'Amérique Méridionale*. Volume 5, part 3: *Mollusques*. Paris: P. Bertrand.
- Dye, A.H., 1988. Rocky shore surveillance on the Transkei Coast, Southern Africa: temporal and spatial variability in the balanoid zone at Dwesa. *South African Journal of Marine Science* 7: 87–99.
- Endean, R., R. Kenny & W. Stephenson, 1956. The ecology and distribution of intertidal organisms on the rocky shores of the Queensland mainland. *Australian Journal of Marine and Freshwater Research* 7: 88–146.
- Etheridge, R., 1889. The general zoology of Lord Howe Island. *Australian Museum Memoirs* 2: 22–31.
- Eyre, J., 1939. The South African intertidal zone and its relation to ocean currents. VII. An area in False Bay. *Annals of the Natal Museum* 9: 283–306.
- Eyre, J., G.J. Broekhuysen & M.I. Crichton, 1938. The South African intertidal zone and its relation to ocean currents. VI. The East London district. *Annals of the Natal Museum* 9: 83–111.
- Eyre, J., & T.A. Stephenson, 1938. The South African intertidal zone and its relation to ocean currents. V. A sub-tropical Indian Ocean shore. *Annals of the Natal Museum* 9: 21–46.
- Finlay, H.J., 1927. A further commentary on New Zealand molluscan systematics. *Transactions of the New Zealand Institute* 57: 320–485.
- Finlay, H.J., 1928. The Recent Mollusca of the Chatham Islands. *Transactions and Proceedings of the New Zealand Institute* 59: 232–286.
- Finlay, H.J., 1930. Additions to the Recent molluscan fauna of New Zealand. *Transactions of the New Zealand Institute* 61: 222–225.
- Fischer, P.H., 1969. Répartition et écologie de *Nodilittorina nodulosa* (Gmelin). *Journal de Conchyliologie* 107: 119–129.
- Fischer, P.H., 1967. Étude critique sur *Nodilittorina nodulosa* (Gmelin) et sur les formes affines. *Journal de Conchyliologie* 106: 47–80.
- Foster, B.A., 1966. The effects of wave exposure and aspect on the vertical shore distribution and population composition of *Melarhapha oliveri*. *Tane* 12: 37–44.
- Gatliff, J.H., 1887. A list of some of the shells of the marine Mollusca found upon the Victorian coast. Part I. *Victorian Naturalist* 4: 57–60.
- Gmelin, J.F., 1791. *Caroli a Linné ... Systema Naturae per Regna Tria Naturae*. Edition 13. Volume 1, part 6. Lugduni.
- Gosliner, T.M., 1981. Origins and relationships of primitive members of the Opisthobranchia (Mollusca: Gastropoda). *Biological Journal of the Linnean Society* 16: 197–225.
- Grant, W.S., & M. Lang, 1991. Mode of larval development and genetic population structure in *Nodilittorina africana knysnaensis* (Prosobranchia: Littorinidae). *Marine Biology* 109: 479–483.
- Gray, J.E., 1826. Mollusca. In *Narrative of a Survey of the Intertropical and Western Coasts of Australia. Performed between the years 1818 and 1822*, ed. P.P. King, pp. 474–496. London: John Murray.
- Guiler, E.R., 1951. Notes on the intertidal ecology of the Freycinet Peninsula. *Papers and Proceedings of the Royal Society of Tasmania* 1950: 53–70.
- Guiler, E.R., 1952a. The ecological features of certain sheltered intertidal areas in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 86: 1–11.

- Guiler, E.R., 1952b. The intertidal ecology of the Eaglehawk Neck Area. *Papers and Proceedings of the Royal Society of Tasmania* 86: 13–29.
- Guiler, E.R., 1952c. The nature of intertidal zonation in Tasmania. *Papers and Proc. Royal Society of Tasmania* 86: 31–61.
- Guiler, E.R., 1955. Australian intertidal belt-forming species in Tasmania. *Journal of Ecology* 43: 138–148.
- Guiler, E.R., 1958. A note on the identity of the Tasmanian littorinid molluscs. *Papers and Proceedings of the Royal Society of Tasmania* 92: 139.
- Haacke, W., 1885. Über Standortvarietäten der südaustralischen *Littorina unifasciata*. *Zoologischer Anzeiger* 8: 504–505.
- Hannaford Ellis, C.J., 1979. Morphology of the oviparous rough winkle *Littorina arcana* Hannaford Ellis, 1978, with notes on the taxonomy of the *L. saxatilis* species-complex (Prosobranchia: Littorinidae). *Journal of Conchology* 30: 43–56.
- Hedley, C., 1910. The marine fauna of Queensland. *Report of the Australian Association for the Advancement of Science* 12: 329–371.
- Hedley, C., 1913. Studies on Australian Mollusca. Part XI. *Proc. Linnean Society of New South Wales* 38: 258–339.
- Hedley, C., 1916. A preliminary index of the Mollusca of Western Australia. *Journal and Proceedings of the Royal Society of Western Australia* 1: 152–226.
- Hedley, C., 1918. A check-list of the marine fauna of New South Wales. Part I.—Mollusca. *Journal and Proceedings of the Royal Society of New South Wales* 51 (Supplement): M1–M120.
- Heller, J., 1975. The taxonomy of some British *Littorina* species with notes on their reproduction (Mollusca: Prosobranchia). *Zoological Journal of the Linnean Society* 56: 131–151.
- Herbert, D.G., & A. Warén, 1999. South African Mollusca described by Ferdinand Krauss: their current status and notes on type material housed in the Naturhistoriska Riksmuseet, Stockholm. *Annals of the Natal Museum* 40: 205–243.
- Hughes, R.N., 1979. On the taxonomy of *Littorina africana* (Mollusca: Gastropoda). *Zoological Journal of the Linnean Society* 65: 111–118.
- Hutton, F.W., 1878. Révision des coquilles de la Nouvelle-Zélande et des îles Chatham. *Journal de Conchyliologie* 26: 1–57.
- Hutton, F.W., 1880. *Manual of the New Zealand Mollusca*. Wellington: Colonial Museum and Geological Survey Department.
- Hutton, F.W., 1882. Notes on some branchiate Mollusca. *Transactions and Proceedings of the New Zealand Institute* 14: 162–167.
- International Commission on Zoological Nomenclature, 1999. *International Code of Zoological Nomenclature*. Edition 4. London: International Trust for Zoological Nomenclature.
- Iredale, T., 1910. On marine mollusca from the Kermadec Islands, and on the “sinusigera apex”. *Proceedings of the Malacological Society of London* 9: 68–79.
- Iredale, T., 1912. New generic names and new species of marine Mollusca. *Proceedings of the Malacological Society of London* 10: 217–228.
- Iredale, T., 1915. A commentary on Suter’s Manual of the New Zealand Mollusca. *Transactions and Proceedings of the New Zealand Institute* 47: 417–497.
- Iredale, T., 1924. Results from Ray Bell’s molluscan collections. *Proceedings of the Linnean Society of New South Wales* 49: 179–278.
- Iredale, T., & J. Allan, 1940. A review of the relationships of the Mollusca of Lord Howe Island. *Australian Zoologist* 9: 444–451.
- Iredale, T., & D.F. McMichael, 1962. A reference list of the marine Mollusca of New South Wales. *Memoirs of the Australian Museum* 11: 1–109.
- Jansen, P., 1995. *Seashells of Central New South Wales*. Townsville.
- Janus, H., 1961. Die Typen und Typoide südafrikanischer Meeresmollusken im Staatlichen Museum für Naturkunde in Stuttgart. I. Gastropoda. *Stuttgarter Beiträge zur Naturkunde aus dem Staatlichen Museum für Naturkunde in Stuttgart* 70: 1–19.
- Jernakoff, P., 1983. Factors affecting the recruitment of algae in a midshore region dominated by barnacles. *Journal of Experimental Marine Biology and Ecology* 67: 17–31.
- Johnston, T.H., 1917. Ecological notes on the littoral fauna and flora of Caloundra, Queensland. *Queensland Naturalist* 2: 53–63.
- Kadolsky, D., 1971. Nomenklatorische Bemerkungen. *Archiv für Molluskenkunde* 101: 191–193.
- Kensley, B., & M.-L. Penrith, 1980. The constitution of the fauna of rocky intertidal shores of South West Africa. Part III. The north coast from False Cape Frio to the Kunene River. *Cimbebasia. Series A* 5: 201–214.
- Kershaw, R.C., 1955. A systematic list of the Mollusca of Tasmania, Australia. *Papers and Proceedings of the Royal Society of Tasmania* 89: 289–355.
- Kershaw, R.C., 1958. Tasmanian intertidal Mollusca. *Journal of the Malacological Society of Australia* 2: 58–100.
- Kilburn, R.N., 1972. Taxonomic notes on South African marine Mollusca (2), with the description of new species and subspecies of *Conus*, *Nassarius*, *Vexillum* and *Demoulia*. *Annals of the Natal Museum* 21: 391–437.
- Kilburn, R., & F. Rippey, 1982. *Sea Shells of Southern Africa*. Johannesburg: Macmillan South Africa.
- Knox, G.A., 1953. The intertidal ecology of Taylor’s Mistake, Banks Peninsula. *Transactions of the Royal Society of New Zealand* 81: 189–220.
- Krauss, F., 1848. *Die Südafrikanischen Mollusken*. Stuttgart: Ebner & Seubert.
- Küster, H.C., 1853–1856. Die Gattung *Littorina*. In *Systematisches Conchylien-Cabinet von Martini und Chemnitz*. Parts 129 (1853, pls. 1, 2), 149 (1856, pls. 3–5, pp. 1–24), ed. H.C. Küster. Nürnberg: Bauer & Raspe.
- Lamarck, J.-B., 1822. *Histoire Naturelle des Animaux Sans Vertèbres*. Volume 7. Paris.
- Ludbrook, N.H., & K.L. Gowlett-Holmes, 1989. Chitons, gastropods and bivalves. In *Marine Invertebrates of Southern Australia. Part II*, ed. S.A. Shepherd & I.M. Thomas, pp. 504–724. Adelaide: South Australian Government.
- Macpherson, J.H., & E.H. Chapple, 1951. A systematic list of the marine and estuarine Mollusca of Victoria. *Memoirs of the National Museum of Victoria* 17: 107–185.
- Macpherson, J.H., & C.J. Gabriel, 1962. *Marine Molluscs of Victoria*. Melbourne: Melbourne University Press.
- Markel, R.D., 1971. Temperature relations in two species of west American littorines. *Ecology* 52: 1126–1130.
- Martens, E.von, 1897. Süß- und Brackwasser-Mollusken des Indischen Archipels. In *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien*, ed. M. Weber, volume 4. Leiden: E.J. Brill.
- May, W.L., 1909. Additions to the Tasmania molluscan fauna. *Papers and Proceedings of the Royal Society of Tasmania* 1908: 53–59.
- May, W.L., 1921. *A Check-list of the Mollusca of Tasmania*. Hobart: Government Printer.
- May, W.L., 1923. *W. L. May’s Illustrated Index of Tasmanian Shells*. Hobart.
- McMahon, R.F., 1992. Microgeographic variation in the shell morphometries of *Nodilittorina unifasciata* from southwestern Australia in relation to wave exposure of shore. In *Proceedings of the Third International Symposium on Littorinid Biology*, ed. J. Grahame, P.J. Mill & D.G. Reid, pp. 107–117. London: Malacological Society of London.
- McMichael, D.F., 1959. Notes on littorinid nomenclature. *Journal of the Malacological Society of Australia* 3: 25–28.
- McQuaid, C.D., 1981a. Population dynamics of *Littorina africana knysnaensis* (Philippi) on an exposed rocky shore. *Journal of Experimental Marine Biology and Ecology* 54: 65–76.
- McQuaid, C.D., 1981b. The establishment and maintenance of vertical size gradients in populations of *Littorina africana knysnaensis* (Philippi) on an exposed rocky shore. *Journal of Experimental Marine Biology and Ecology* 54: 77–89.

- McQuaid, C.D., 1992. Stress on the high shore: a review of age-dependent causes of mortality in *Nodilittorina knysnaensis* and *N. africana*. In *Proceedings of the Third International Symposium on Littorinid Biology*, ed. J. Grahame, P.J. Mill & D.G. Reid, pp. 85–89. London: Malacological Society of London.
- McQuaid, C.D., 1996a. Biology of the gastropod family Littorinidae. I. Evolutionary aspects. *Oceanography and Marine Biology Annual Review* 34: 233–262.
- McQuaid, C.D., 1996b. Biology of the gastropod family Littorinidae. II. Role in the ecology of intertidal and shallow marine ecosystems. *Oceanography and Marine Biology Annual Review* 34: 263–302.
- McQuaid, C.D., & P.A. Scherman, 1988. Thermal stress in a high shore intertidal environment: morphological and behavioural adaptations of the gastropod *Littorina africana*. In *Behavioural Adaptations to Intertidal Life. NATO ASI Series. Series A: Life Sciences*, ed. G. Chelazzi & M. Vannini, pp. 213–224. New York: Plenum Press.
- Menke, K.T., 1843. *Molluscorum Novae Hollandiae Specimen*. Hannover: Libraria Aulica Hahniana.
- Menke, K.T., 1844. *Molluscorum Novae Hollandiae specimen*. *Zeitschrift für Malakozoologie* 1844: 52–64.
- Montagu, G., 1815. An account of some new and rare marine British shells and animals. *Transactions of the Linnean Society of London* 11: 179–204.
- Morton, J.E., 1975. Form and habit in some small gastropods of New Zealand boulder beaches. *Veliger* 18: 1–15.
- Morton, J., & M. Miller, 1968. *The New Zealand Sea Shore*. London: Collins.
- Nevill, G., 1885. *Hand List of Mollusca in the Indian Museum, Calcutta. Part 2*. Calcutta: Indian Museum.
- Newman, S., 1994. *Comparative biology of two Tasmanian Nodilittorina*. Hons thesis, University of Tasmania.
- Nwe, T., 1974. *Littorina unifasciata Gray and L. praetermissa May (Mesogastropoda, Littorinidae) in South Australia*. PhD thesis, University of Adelaide.
- Oliver, W.R.B., 1915. The Mollusca of the Kermadec Islands. *Transactions of the New Zealand Institute* 47: 509–568.
- Penrith, M.-L., & B. Kensley, 1970a. The constitution of the intertidal fauna of rocky shores of South West Africa. Part I. Lüderitzbucht. *Cimbebasia. Series A* 1: 191–239.
- Penrith, M.-L., & B. Kensley, 1970b. The constitution of the fauna of the rocky intertidal shores of South West Africa. Part II. Rocky Point. *Cimbebasia. Series A* 1: 243–268.
- Philippi, R.A., 1845–1850. *Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien*. Cassel: Theodor Fischer.
- Pilkington, M.C., 1971. Eggs, larvae and spawning in *Melarapha cincta* (Quoy and Gaimard) and *M. oliveri* Finlay (Littorinidae: Gastropoda). *Australian Journal of Marine and Freshwater Research* 22: 79–90.
- Ponder, W.F., G.A. Clark, A. Miller & A. Toluzzi, 1993. On a major radiation of freshwater snails in Tasmania and eastern Victoria—a preliminary overview of the *Beddomeia* group (Mollusca: Gastropoda: Hydrobiidae). *Invertebrate Taxonomy* 7: 501–750.
- Ponder, W.F., & J. Rosewater, 1979. Rectifications in the nomenclature of some Indo-Pacific Littorinidae. *Proceedings of the Biological Society of Washington* 92: 773–782.
- Ponder, W.F., & F.E. Wells, 1998. Distribution and relationships of marine and estuarine fauna. In *Mollusca: the Southern Synthesis. Fauna of Australia*, ed. P.L. Beesley, G.J.B. Ross & A. Wells, pp. 77–80. Melbourne: CSIRO Publishing.
- Potter, C.M., 1987. Aspects of the biology of Natal Littorinidae: I: population dispersion and microhabitat selection. *Investigational Report of the Oceanographic Research Institute, Durban* 65: 1–15.
- Potter, C.M., & M.N. Schleyer, 1991. Aspects of the biology of Natal Littorinidae: II. Feeding and food availability. *Investigational Report of the Oceanographic Research Institute, Durban* 66: 1–15.
- Powell, A.W.B., 1933a. The high-tidal Mollusca of Rangitoto Island, Auckland; with descriptions of a new genus and two new species. *Transactions and Proceedings of the New Zealand Institute* 63: 144–152.
- Powell, A.W.B., 1933b. The marine Mollusca of the Chatham Islands. *Records of the Auckland Institute Museum* 1: 181–208.
- Powell, A.W.B., 1937. *The Shellfish of New Zealand. An Illustrated Handbook*. Auckland: Unity Press.
- Powell, A.W.B., 1955. Mollusca of the Southern Islands of New Zealand. *New Zealand Department of Scientific and Industrial Research. Cape Expedition Bulletin* 15: 1–138.
- Powell, A.W.B., 1962. *Shells of New Zealand. An Illustrated Handbook*. Edition 4. Christchurch: Whitcombe & Tombs.
- Powell, A.W.B., 1976. *Shells of New Zealand. An Illustrated Handbook*. Edition 5. Christchurch: Whitcoulls Publishers.
- Powell, A.W.B., 1979. *New Zealand Mollusca*. Auckland: Collins.
- Pritchard, G.B., & J.H. Gatliff, 1902. Catalogue of the marine shells of Victoria. Part 5. *Proceedings of the Royal Society of Victoria* 14: 85–138.
- Quoy, J.R.C., & J.P. Gaimard, 1833. *Voyage de Découvertes de l'Astrolabe. Zoologie*, vol. 2. Paris.
- Reeve, L.A., 1857–1858. Monograph of the genus *Littorina*. In *Conchologia Iconica*, ed. L.A. Reeve, pls. 1–16 (1857), 17–18 (1858). London: Lovell Reeve.
- Reid, D.G., 1986. *The Littorinid Molluscs of Mangrove Forests in the Indo-Pacific Region: the Genus Littoraria*. London: British Museum (Natural History).
- Reid, D.G., 1989. The comparative morphology, phylogeny and evolution of the gastropod family Littorinidae. *Philosophical Transactions of the Royal Society of London. Series B* 324: 1–110.
- Reid, D.G., 1992. The gastropod family Littorinidae in Hong Kong. In *Proceedings of the Fourth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China III*, ed. B. Morton, pp. 187–210. Hong Kong: Hong Kong University Press.
- Reid, D.G., 1996. *Systematics and Evolution of Littorina*. London: Ray Society.
- Reid, D.G., 1998. Family Littorinidae. In *Mollusca: the Southern Synthesis. Fauna of Australia*, volume 5, ed. P.L. Beesley, G.J.B. Ross & A. Wells, pp. 738–739. Melbourne: CSIRO Publishing.
- Reid, D.G., 1999. The genus *Littoraria* Griffith & Pidgeon, 1834 (Gastropoda: Littorinidae) in the tropical eastern Pacific. *Veliger* 42: 21–53.
- Reid, D.G., 2001. The genus *Nodilittorina* von Martens, 1897 (Gastropoda: Littorinidae) in the Indo-Malayan region. *Phuket Marine Biological Center Special Publication* 25: 433–449.
- Reid, D.G., 2002a. The genus *Nodilittorina* von Martens, 1897 (Gastropoda: Littorinidae) in the eastern Pacific Ocean, with a discussion of biogeographic provinces of the rocky-shore fauna. *Veliger* 45: 85–170.
- Reid, D.G., 2002b. Morphological review and phylogenetic analysis of *Nodilittorina* (Gastropoda: Littorinidae). *Journal of Molluscan Studies* 68: 259–281.
- Reid, D.G., & J.B. Geller, 1997. A new ovoviparous species of *Tectarius* (Gastropoda: Littorinidae) from the tropical Pacific, with a molecular phylogeny of the genus. *Journal of Molluscan Studies* 63: 207–233.
- Reid, D.G., & Y.-M. Mak, 1998. Additions and corrections to the taxonomy of the genus *Peasiella* Nevill, 1885 (Gastropoda: Littorinidae). *Nautilus* 112: 6–33.
- Reid, D.G., E. Rumbak & R.H. Thomas, 1996. DNA, morphology and fossils: phylogeny and evolutionary rates of the gastropod genus *Littorina*. *Philosophical Transactions of the Royal Society of London. Series B* 351: 877–895.
- Rosewater, J., 1970. The family Littorinidae in the Indo-Pacific. Part I. The subfamily Littorininae. *Indo-Pacific Mollusca* 2: 417–506.

- Rudman, W.B., 1996. A note on the egg capsule of *Nodilittorina unifasciata* from eastern Australia. *Molluscan Research* 17: 111–114.
- Schneider, B., 2003. Littorinidae in WA's South West. *WA Shell Collector* 9(4): 3–7.
- Schniebs, K., 2000. Die Typen und Typoide de Molluskensammlung des Staatlichen Museums für Tierkunde Dresden (I). Die Typen der von Anton (1838) beschriebenen rezenten Mollusken: 5. Phasianellidae, Littorinidae, Thiaridae, Cerithiidae, Turritellidae, Ranellidae, Olividae, Actintinellidae. *Malakologische Abhandlungen* 20: 79–87.
- Smith, E.A., 1884. Mollusca. In *Report on the Zoological Collections Made in the Indo-Pacific Ocean During the Voyage of H.M.S. "Alert" 1881–2*, pp. 34–116. London: British Museum.
- Smith, E.A., 1892. Descriptions of new species of shells from New South Wales, New Guinea, the Caroline and Solomon Islands. *Proceedings of the Zoological Society of London* 1891: 486–491.
- Sowerby, G.B., 1892. *Marine Shells of South Africa*. London: Sowerby.
- Spencer, H.G., & R.C. Willan, 1996. The marine fauna of New Zealand: Index to the fauna. 3. Mollusca. *New Zealand Oceanographic Institute Memoir* 105: 1–125.
- Stephenson, T.A., 1944. The constitution of the intertidal fauna and flora of South Africa. Part II. *Annals of the Natal Museum* 10: 261–358.
- Stephenson, T.A., 1947. The constitution of the intertidal fauna and flora of South Africa. Part III. *Annals of the Natal Museum* 11: 207–324.
- Stephenson, T.A., A. Stephenson & J.H. Day, 1940. The South African intertidal zone and its relation to ocean currents, VIII. Lamberts Bay and the West Coast. *Annals of the Natal Museum* 9: 345–380.
- Stephenson, T.A., A. Stephenson & C.A. du Toit, 1937. The South African intertidal zone and its relation to ocean currents. *Transactions of the Royal Society of South Africa* 24: 341–382.
- Suter, H., 1901. List of the species described in F.W. Hutton's Manual of the New Zealand Mollusca, with the corresponding names used at the present time. *Transactions of the New Zealand Institute* 34: 207–224.
- Suter, H., 1913. *Manual of the New Zealand Mollusca*. Wellington: Government Printer.
- Tate, R., & W.L. May, 1901. A revised census of the marine Mollusca of Tasmania. *Proceedings of the Linnean Society of New South Wales* 1901: 344–471.
- Tenison Woods, J.E., 1878. Census; with brief descriptions of the marine shells of Tasmania and the adjacent islands. *Papers and Proceedings of the Royal Society of Tasmania* 1877: 26–57.
- Tenison Woods, J.E., 1879. On some Australian Littorinidae. *Proceedings of the Linnean Society of New South Wales* 3: 55–72.
- Thiele, J., 1929. *Handbuch der Systematischen Weichtierkunde*. Part I. Jena: Gustav Fischer.
- Tomlin, J.R.le B., 1923. On South African marine Mollusca with descriptions of several new species. *Journal of Conchology* 17: 40–52.
- Troschel, F.H., 1856–1863. *Das Gebiss der Schnecken*. Berlin: Nicolaische Verlagsbuchhandlung.
- Tryon, G.W., 1887. *Manual of Conchology*. Volume 9. Philadelphia.
- Turton, W.H., 1932. *The Marine Shells of Port Alfred, South Africa*. Oxford: Oxford University Press.
- Underwood, A.J., 1974. The reproductive cycle and geographical distribution of some common eastern Australian prosobranchs (Mollusca: Gastropoda). *Australian Journal of Marine and Freshwater Research* 25: 63–88.
- Underwood, A.J., 1981. Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. *Journal of Experimental Marine Biology and Ecology* 51: 57–85.
- Underwood, A.J., & M.G. Chapman, 1985. Multifactorial analyses of directions of movement of animals. *Journal of Experimental Marine Biology and Ecology* 91: 17–43.
- Underwood, A.J., & M.G. Chapman, 1989. Experimental analyses of the influence of topography of the substratum on movements and density of an intertidal snail, *Littorina unifasciata*. *Journal of Experimental Marine Biology and Ecology* 134: 175–196.
- Underwood, A.J., & M.G. Chapman, 1992. Experiments on topographic influences on density and dispersion of *Littorina unifasciata* in New South Wales. In *Proceedings of the Third International Symposium on Littorinid Biology*, ed. J. Grahame, P.J. Mill & D.G. Reid, pp. 181–185. London: Malacological Society of London.
- Underwood, A.J., & M.G. Chapman, 1996. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107: 212–224.
- Underwood, A.J., & K.E. McFadyen, 1983. Ecology of the intertidal snail *Littorina acutispira* Smith. *Journal of Experimental Marine Biology and Ecology* 66: 169–197.
- Verco, J.C., 1908. *Catalogue of marine Mollusca of South Australia*. Adelaide.
- Vermeij, G.J., 1973. Morphological patterns in high intertidal gastropods: adaptive strategies and their limitations. *Marine Biology* 20: 319–346.
- Watson, R.B., 1886. Report on the Scaphopoda and Gasteropoda collected by H.M.S. Challenger during the years 1873–76. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76. Zoology* 15: 1–756.
- Weinkauff, H.C., 1878, 1882. Die Gattung *Litorina*. Angefangen von Dr. Küster, durchgesehen, ergänzt und vollendet von H.C. Weinkauff. *Systematisches Conchylien-Cabinet von Martini und Chemnitz*. Parts 269 (pp. 25–40, 1878), 315 (pp. 41–72, pls 6–11, 1882), 318 (pp. 73–114, pls 12–14, 1882). Nürnberg: Bauer & Raspe.
- Weinkauff, H.C., 1883. Catalog der Gattung *Litorina* Férussac. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft nebst Nachrichtenblatt* 10: 213–227.
- Wells, F.E., 1980. The distribution of shallow-water marine prosobranch gastropod molluscs along the coastline of Western Australia. *Veliger* 22: 232–247.
- Wells, F.F., 1984. Population characteristics of the periwinkle, *Nodilittorina unifasciata*, on a vertical rock cliff in Western Australia. *Nautilus* 98: 102–107.
- Wenz, W., 1938. Gastropoda. Teil I: Allgemeiner Teil und Prosobranchia. In *Handbuch der Paläozoologie*, ed. O.H. Schindewolf, volume 6. Berlin: Gebrüder Borntraeger.
- Williams, S.T., D.G. Reid & D.T.J. Littlewood, 2003. A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism and biogeography of the Southern Ocean. *Molecular Phylogenetics and Evolution* 28: 60–86.
- Wilson, B., 1993. *Australian Marine Shells. Prosobranch Gastropods*. Part 1. Kallaroo: Odyssey Publishing.
- Wilson, B.R., & G.R. Allen, 1987. Major components and distribution of marine fauna. In *Fauna of Australia, General Articles*, volume 1A, ed. G.R. Dyne & D.W. Walton, pp. 43–68. Canberra: Australian Government Publishing Service.
- Wilson, B.R., & K. Gillett, 1971. *Australian Shells*. Sydney: A.H. & A.W. Reed.
- Wilson, B.R., & K. Gillett, 1979. *A Field Guide to Australian Shells. Prosobranch Gastropods*. Sydney: A.H. & A.W. Reed.
- Womersley, H.B.S., & S.J. Edmonds, 1958. A general account of the intertidal ecology of South Australian coasts. *Australian Journal of Marine and Freshwater Research* 9: 217–260.

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